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Life in the World's Oceans

Course Guidebook

Professor Sean K. Todd
College of the Atlantic



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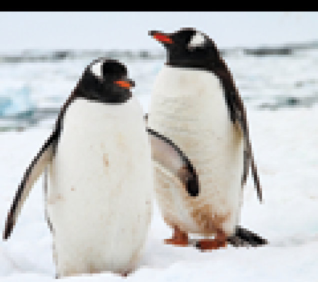
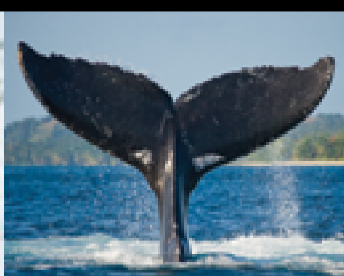


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Steven K. Katona Chair in Marine Sciences

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Sean K. Todd holds the Steven K. Katona Chair in Marine Sciences at College of the Atlantic, a 4-year undergraduate and graduate college in Bar Harbor, Maine, that focuses on transdisciplinary studies in human ecology. Professor Todd received a Joint Honours undergraduate degree in Marine Biology and Oceanography from Bangor University in the United Kingdom. He received his master's and doctoral degrees in Biopsychology at Memorial University of Newfoundland in St. John's, Newfoundland and Labrador, Canada. While at Memorial University, Professor Todd worked as a sessional instructor in foundational biology and biostatistics. He was then hired by College of the Atlantic as a faculty member in Biology & Marine Mammals and became the inaugural holder of the Steven K. Katona Chair in Marine Sciences in 2006. In that same year, Professor Todd also became director of Allied Whale, the college's marine mammal research program, which includes the Marine Mammal Stranding Response Program, one of two programs responsible for stranding response in Maine. In 2008, he became the Associate Dean of Graduate Studies, a position he held until 2016. In addition, since 2001, he has worked part time on board ecotourism expedition vessels as a professional guide and lecturer specializing in Antarctic guiding.

Professor Todd has had a number of diverse marine mammal research interests for the past 30 years that can be divided into 4 broad realms: foraging ecology, population studies, bioacoustics, and fishery interactions. He is particularly interested in the intersection between rorqual whale trophic dynamics and oceanographic regime shifts. Professor Todd's interest in population studies derives from his work with various photo-identification catalogs curated by Allied Whale, and he is a significant contributor to the Antarctic Humpback Whale Catalogue, helping to coordinate a citizen science program of humpback whale photo-identification from expedition vessels operating in the Southern Ocean. Professor Todd's bioacoustics work uses passive acoustic monitoring to determine marine mammal distribution, and his work with fishery interactions aims to mitigate conflicts between the fishing industry and marine mammals. He presents frequently at internationally based professional conferences.

In 1998, Professor Todd received the Birks Medal from Memorial University in recognition of his student leadership within the School of Graduate Studies. In 2005, he received, on behalf of the Marine Mammal Stranding Response Program that he directs, the David St. Aubin Award for recognition of leadership in the marine mammal stranding response community. Professor Todd is an appointed member of the scientific advisory board for the Marine & Environmental Research Institute and was a member of the scientific advisory council for the American Cetacean Society.

Professor Todd has authored or coauthored a variety of peer-reviewed papers for several journals, including *Bioacoustics*, the *Canadian Journal of Zoology*, *Endangered Species Research*, the *Journal of the Acoustical Society of America*, *Marine Mammal Science*, the *Journal of the Marine Biological Association of the United Kingdom*, *Marine Policy*, and the *Journal of Northwest Atlantic Fishery Science*. He has also completed several invited chapters for various books, including *Marine Mammal Sensory Systems* and *Sensory Abilities of Cetaceans: Laboratory and Field Evidence*. His work has been featured by the BBC Natural History Unit, CBC, National Public Radio, *Scientific American Frontiers*, and PBS's *QUEST*. ◆

ABOUT OUR PARTNER

Founded in 1846, the Smithsonian is the world's largest museum and research complex, consisting of 19 museums and galleries, the National Zoological Park, and 9 research facilities. The total number of artifacts, works of art, and specimens in the Smithsonian's collections is estimated at 154 million. These collections represent America's rich heritage, art from across the globe, and the immense diversity of the natural and cultural world.

In support of its mission—the increase and diffusion of knowledge—the Smithsonian has embarked on four Grand Challenges that describe its areas of study, collaboration, and exhibition: Unlocking the Mysteries of the Universe, Understanding and Sustaining a Biodiverse Planet, Valuing World Cultures, and Understanding the American Experience. The Smithsonian's partnership with The Great Courses is an engaging opportunity to encourage continuous exploration by learners of all ages across these diverse areas of study.

In this course, *Life in the World's Oceans*, The Great Courses teams with the Smithsonian Institution to produce a vivid exploration of oceanic life—from tiny unicellular organisms to enormous whales. One of the world's leading marine biologists introduces you to life in the marine environment, covering the basics of the marine food chain before focusing the bulk of the course on some of the ocean's most fascinating creatures, including seals, dolphins, sharks, and whales. Along the way, you learn lessons in the evolution of marine biology since the oceans gave rise to Earth's earliest life-forms approximately 4 billion years ago. Lectures are filled with stunning imagery from many of the field's most fascinating areas of study, including bioluminescence, and the Smithsonian's own cutting-edge research work around the world, including on the Great Barrier Reef. ◆

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SUPPLEMENTARY MATERIAL

LIFE IN THE WORLD'S OCEANS

The Earth's ocean is its most significant feature. Taking up more than 70% of the Earth's surface, our ocean is essential for life on this planet. It provides approximately 2/3 of the oxygen we breathe, and it helps control and regulate our climate. Life on this planet evolved in our ocean almost 4 billion years ago. The ocean has nurtured life ever since, to the point today that 25% of all species on this planet currently lives in the ocean, although scientists believe that we may have only discovered 10% of the ocean's species diversity. This course uses an ecological perspective to review the extraordinary diversity of life in the ocean, ultimately examining the extraordinary diversity of marine mammals that act as apex predators in this fascinating ecosystem.

The first section of the course briefly reviews the physics of water and basic physical oceanography so that you may understand the key differences between a marine and terrestrial ecosystem. You will learn about the unique chemistry of water that is so fundamental to life on this planet and use the knowledge to gain a more general understanding of physical ocean systems.

In the second section, you will consider basic ecosystems within the marine environment, including shelves, beaches, estuaries, coral reefs, the abyss, and the polar regions. You will examine the life in them, focusing on lower trophic levels that include prokaryotic picoplankton and nanoplankton as well as eukaryotic

phytoplankton and zooplankton. This section focuses more on invertebrate animals, although it concludes with a brief examination of vertebrate marine life.

The third section focuses more closely on marine vertebrates, examining cartilaginous and bony fish, sea turtles, and marine birds. You will review human's relationship to each of these groups and consider the importance of anthropogenic biological resource extraction on the sustainability of these species.

The fourth section focuses exclusively on marine mammals, a polyphyletic grouping of animals representing 5 separate evolutionary incursions from the terrestrial environment back to the ocean. You will examine in depth the challenges of living in a marine environment and the solutions—morphological, physiological, and behavioral—that marine mammals have adopted over evolutionary time through the process of natural selection. You will review the ever-developing relationship between humans and marine mammals, both positive and negative, including whale hunts, conflicts in fisheries, strandings, and issues of captivity.

The fifth and final section looks to the future of the ocean. You will consider our current relationship with the planet and examine its sustainability by reviewing the impacts of climate change, ocean acidification, and overfishing. The course ends with a call to arms for action, for us—as citizens of this planet—to save the ocean, this awe-inspiring and profoundly important environment that has nurtured life on this planet for so long. ◆

1

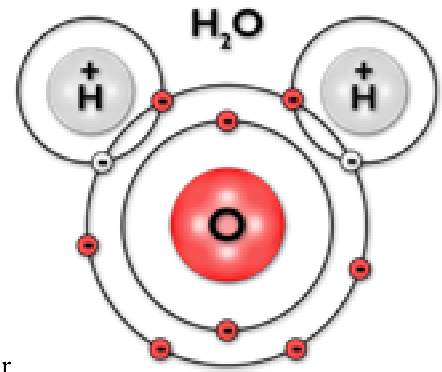
WATER: THE SOURCE OF LIFE

Everything on our planet depends on the unique chemical properties of water. We are more than fortunate that the surface of our planet is comprised mostly of water. If it wasn't, life could not have evolved in the way that it has to create the incredible diversity we see today. The topic of this lecture is water—what it is and why it matters so much.

Water at the Molecular Level

- The chemical formula for water is H_2O, or dihydrogen monoxide. The H stands for hydrogen, which is pretty much the simplest element that we know of, consisting of one positively charged proton orbited by one negatively charged electron. The 2 in the formula means that there are 2 hydrogen atoms in a molecule of water.

- The O stands for oxygen, which consists of 8 electrons orbiting a nucleus of 8 protons and 8 neutrons. Quantum mechanics theory dictates that these electrons are ordered in concentric shells around the nucleus. In oxygen, there are 2 shells, and the first of these, closest to the nucleus, houses 2 electrons. The outer shell contains 6 electrons.



- Although the outer shell contains 6 electrons, it has the capacity to take 8. From the perspective of the oxygen atom, it should try to fill those last 2 slots. The oxygen is desperate for electron donors, and it finds them in hydrogen. Each of those 2 hydrogens is willing to share its electron with the outer shell of oxygen. The technical name for this sharing is called a covalent bond, and it's extremely strong once formed. In other words, it's very hard to break apart water molecules.

◇ Covalent bonds are a common phenomenon in chemistry, but water turns out to have very special covalent bonds. The oxygen atom so wants those last 2 electrons to complete its outer shell that it ends up pulling them slightly away from the hydrogen atoms.

◇ This means that the oxygen end of a water molecule is slightly more negatively charged and the hydrogen in the molecule is slightly more positively charged than one might expect. In chemistry, this is called polarity. Essentially, water is a polar molecule. And this polarity is what makes water such a fundamental ingredient for life.

◇ The polarity of water molecules leads to 5 very important properties that are essential for life: water's elevated melting and boiling points, its unusual ability to absorb energy without increasing temperature, a unique relationship between temperature and density, its unusual cohesive and adhesive properties, and its role as a universal solvent.

1. Pure water freezes at 0° Celsius and boils at 100° Celsius. This temperature range is very important. Our planet is positioned not too far away from the Sun, nor too close. In this way, we can experience all phases of water: as ice, steam, and liquid. It is this liquid state that is so essential for life.

2. Water has a remarkable ability to absorb heat and not change that much in temperature. This ability is called its specific heat capacity, and water has a very high specific heat capacity. One reason why the temperatures on our planet are so agreeable to life as we know it is because the ocean acts as a buffer, absorbing some of the heat of the Sun.

3 When one cools liquid water, something unexpected happens. Most chemical compounds tend to increase in density as they cool. This is because less energy in the compound results in the molecules being, on average, closer together. This is also true for water, up to a point. However, as water starts to approach its freezing point, a lattice structure starts to form, regularizing the distance between molecules and preventing the water molecules from getting any closer. As a result, frozen water is actually less dense than liquid water. And because ice is less dense than liquid water, this means that ice will float.

4 Water's cohesive nature and its ability to adhere to a surface have important implications at the cellular level. Capillary action and surface tension are 2 important consequences of this property.

5 Water is often referred to as the universal solvent, which means that water has a high affinity to dissolve many different substances, or solutes. The solutes that can be dissolved also need to be polar in nature, because negative ions will be attracted to the positive hydrogen end of the water molecule and positive ions will be attracted to the negative oxygen end of the molecule.

◇ The chemical name for salt is sodium chloride, and it makes up almost 90% of the salt in the ocean. But there are many other kinds of salts, not as common, also dissolved in the ocean, including those made from magnesium, calcium, and potassium.

◇ Why are the oceans salty? The answer lies in runoff from the land. As our rivers run over the rocks that make up our continents, they partially dissolve those rocks, putting the chemical constituents into solution. Because all rivers lead to the ocean, over a very long time, our oceans have become salty.

NUTRIENTS AND METABOLIC PROCESSES

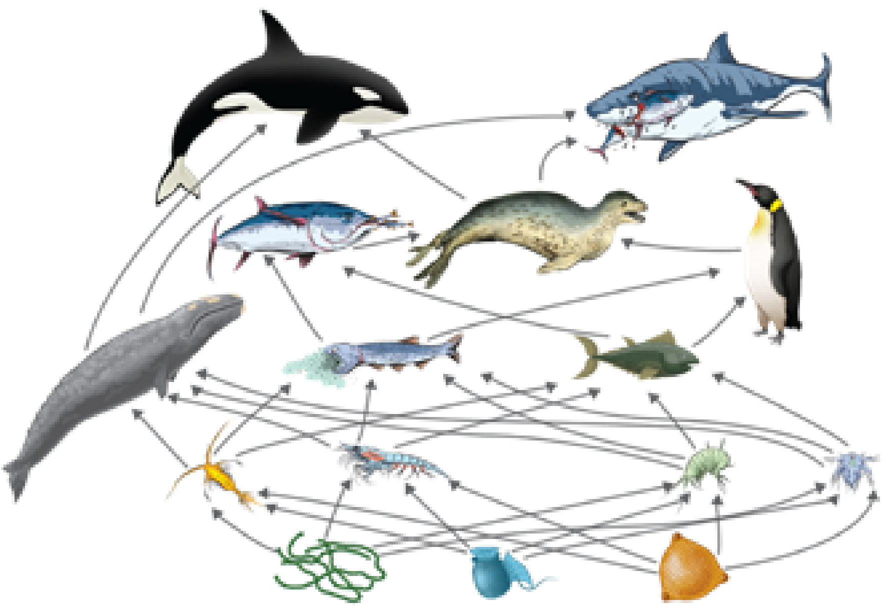
We are made up mostly of water. By weight, our cells are comprised mostly of water in its liquid form. And the presence of liquid water is crucial because it acts as a medium for those compounds essential for the processes of life. The processes of diffusion and osmosis can happen because the water remains in its liquid state, and diffusion of various metabolic products in and out of the cell typically occurs because these products can dissolve in water. Water is essential to life, so much so that we now believe that life evolved initially in water.

- But the ocean contains so much more than just the salt that is dissolved in it. It also contains many different chemicals that are essential to life. By definition, a chemical that is essential to the process of life is called a nutrient.

- But where do nutrients come from? Like salts, some come from river runoff. But mostly nutrients come from dead organisms in the ocean, which through the act of decomposition release these nutrients back into the water. One can characterize this as a cycle: In life, the organism takes up nutrients that are vital for processes of life, and in death, those nutrients are released back to the water.

- Whereas salts are reasonably evenly distributed throughout the ocean, nutrients are not. Because of oceanographic processes, nutrients tend to focus in certain areas. Most importantly, most organisms sink on death, and as they slowly decompose, we can expect relatively high concentrations of nutrients at depth, as compared to the shallows, which will be typically less fertile.

- At the base of every food web is some form of primary producer. In areas where there is sufficient light, that producer is typically a photosynthetic life-form, such as phytoplankton. Photosynthesizers have the ability to use sunlight energy to take simple carbon molecules, such as carbon dioxide, and make more complex energy-rich molecules, such as sugars.



◇ The chemical equation that represents this process of photosynthesis is essentially carbon dioxide and water coming together to make sugar molecules and oxygen. Sugar molecules can then be chemically altered to make all the other organic molecules necessary for life, including proteins, fats, and nucleic acids.

PHOTOSYNTHESIS

$$6CO_2 + 6H_2O \longrightarrow C_6H_{12}O_6 + 6O_2$$

carbon dioxide + water ⟶ glucose + oxygen

◇ But the photosynthesis equation can only happen in the presence of 2 really important conditions. First, we need light. Second, the process of photosynthesis is driven by enzymes, and for those enzymes to work, we need the nutrients that were just mentioned. Those nutrients are available to a photosynthetic cell because they dissolve in water. To get them, all the cell has to do is absorb them from the water.

◇ And this is the paradox: Photosynthetic cells need light and thus must typically stay close to the ocean's surface, yet the nutrients needed for the photosynthetic equation are typically found at depth. How do photosynthetic producers solve this problem? The answer lies in the fact that one only finds such life in areas where there are oceanographic processes that can move nutrient-loaded water from the depths to the surface, a phenomenon called upwelling.

- Because upwelling is an exception rather than the rule, we only find photosynthetic activity in certain places in the ocean. We describe such areas as being productive. In reality, the productivity that is being referred to is photosynthetic activity, but because such activity is essential for the beginnings of a food web, we would also associate these areas with higher concentrations of zooplankton, fish, marine mammals, and other apex predators. In other words, life in the ocean focuses into hot spots.

- All of this starts with the phenomenon of photosynthetic production. But only certain organisms are capable of photosynthesis. On land, we would traditionally restrict this ability to the plants. However, in the water, there technically aren't that many plants. But we do have millions and millions of algal cells, as well as many kinds of bacteria that can perform photosynthesis.

- The potential for our oceans to support photosynthesis through these organisms is vast. In fact, more than half of the oxygen you are breathing right now comes from the oceans, and oxygen is just a by-product of the photosynthesis equation. The real goal of photosynthesis is to create energy-rich macromolecules that can be used to build a cell, or as a source of calories for growth.

- Another important metabolic process is cellular respiration. All cells are capable of this. The act of cellular respiration is somewhat the reverse of photosynthesis. In it, the cell takes complex, energy-rich molecules and breaks them down into their smaller components, thus releasing energy that we can use to do metabolic work.

- The simplest chemical representation of cellular respiration is simply the photosynthesis equation in reverse. In aerobic conditions, a chemically complex sugar molecule is oxidized or burned to produce molecules of carbon dioxide and water, with a net release of energy.

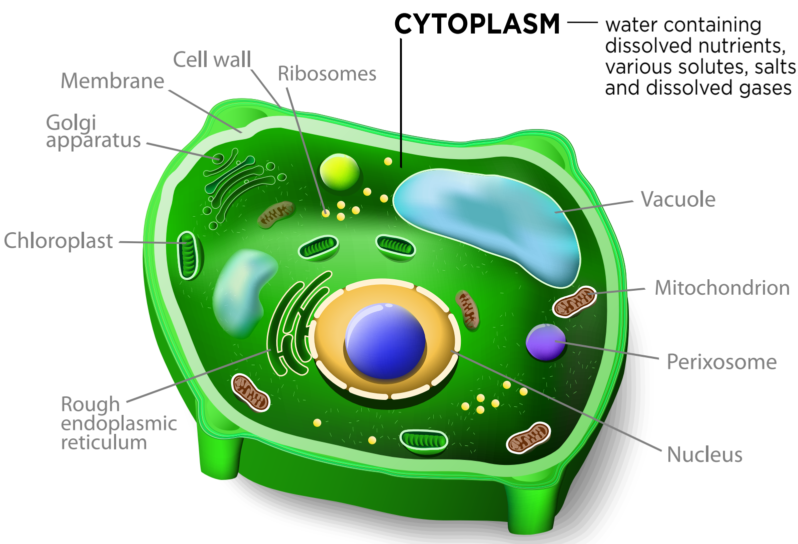
CELLULAR RESPIRATION

$$C_6H_{12}O_6 + 6O_2 \longrightarrow 6CO_2 + 6H_2O + ATP$$

glucose + oxygen ⟶ carbon dioxide + water + energy

- Photosynthesis and cellular respiration are metabolic processes that occur in the chemical soup of the cytoplasm of the cell. And that soup is made up of water containing dissolved nutrients, various solutes, salts, and dissolved gases, such as carbon dioxide and oxygen—all essential for those metabolic processes.

> Water is the essential ingredient in the recipe of life.



Density and the Water Column

◇ The density of an object is a measure of how much mass it has in relation to the volume it occupies. For seawater, density is controlled by 3 factors: temperature, salinity, and pressure.

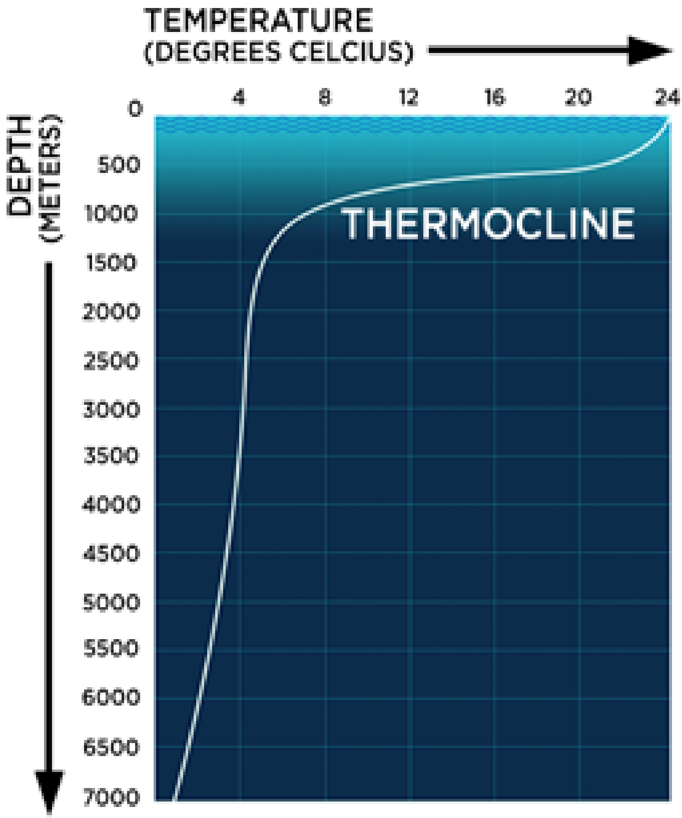
◇ The temperature of seawater is largely controlled by how much radiation it receives from the Sun. In this way, it is logical to assume that seawater will be at its warmest at the equator, on the surface. However, the Sun's energy does not penetrate well into the water column, and the temperature soon decreases as you descend into the depths. Increases in temperature reduce the density of seawater because the increased heat energy causes water molecules to be farther apart from each other.

◇ If we were to graph changes in temperature for the tropics using depth of water as the *y*-axis and temperature as the *x*-axis, we would see a layer of warm, less-dense water floating on top of cooler, denser water, with a dramatic and sharp boundary between the 2. This boundary is called the thermocline, and it represents a front between 2 types of water.

◇ The fact that we can have a condition where a layer of water can float on top of another layer of water might seem strange, but it is a common concept in oceanography. Without agitation, the 2 layers settle out according to their density. Returning to our tropical situation, that difference in density is caused by heat.

◇ Salinity can also affect density, with saltier oceans being denser than fresher oceans. However, unless one is close to a freshwater source, salinity is relatively constant for a given latitude.

◇ And although in general ambient pressure can dramatically affect density, in the case of water it has almost negligible effects because water is relatively incompressible. So, in the case of open



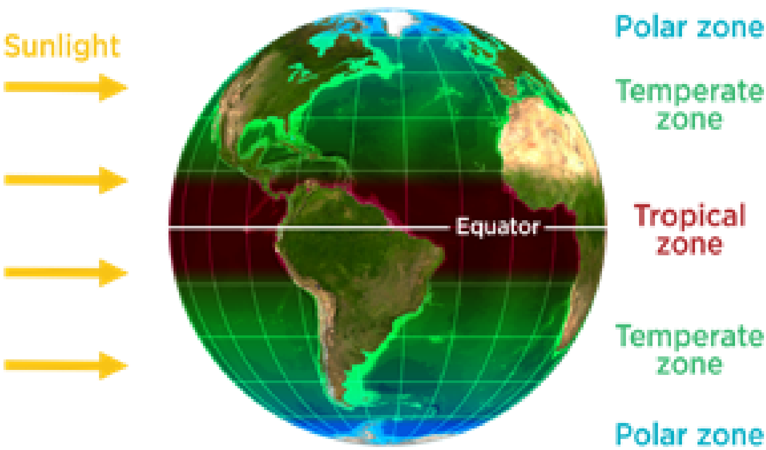
oceans, it is temperature that is driving the differences in density, and the boundary between the 2 types of water is marked by the thermocline.

◇ This stratification of the water column is a well-established trait of equatorial waters. Unless specific oceanographic conditions were to cause an upwelling in the area, the water column remains unmixed, with the shallow, warm waters isolated from the deeper, nutrient-rich water.

- So, contrary to what one might expect, tropical waters are relatively barren of life, at least in terms of biomass. These regions have plenty of light, but they lack the nutrients to sustain photosynthesis. Because of this, such areas are called nutrient limited.

- In the high-latitude polar regions, there is much less radiation from the Sun. So, if any stratification builds up, it is very weak. Also, these areas are stormy. High storm activity acts to break down any stratification that might occur and helps mix the water so that nutrient-rich waters are brought to the surface. These regions are called light limited.

- In the temperate regions, which produce the most biomass, there is a blend of both the tropical and polar systems.



LECTURE SUPPLEMENTS

Readings

Cramer, *Smithsonian Ocean*.

Knowlton, *Citizens of the Sea*.

McIntyre, ed., *Life in the World's Oceans*.

Mora, Tittensor, Adl, Simpson, and Boris, "How Many Species Are There on Earth and in the Ocean?"

Pauly and MacLean, *In a Perfect Ocean*.

Questions to Consider

1. Given the importance of water as an ingredient for life on this planet, what other planets are we investigating that also have water in its liquid form?

2. Think about where the fish you eat comes from. Ask your supermarket if you don't know. Then, research that area in terms of its oceanography. What makes that region productively rich?

3. If you live on the coast, do you live in a temperate, tropical, or polar region? Apply the concepts of productivity to your region; is it light limited, nutrient limited, or both?

2

OCEAN CURRENTS AND WHY THEY MATTER

This lecture focuses on ocean currents—both surface currents and deep currents. What do we know about these currents, and why do they matter? In this lecture, you will learn about 2 types of currents: wind-driven and thermohaline currents, which together create a global circulation of water around the planet's one ocean. These currents have a profound impact on our lives, no matter how far inland we may live. From the food that the ocean can help provide to the very climate in which we live, ocean currents are essential as the engine that drives the mixing of the ocean.

Coriolis Force

- The name "Coriolis force" is somewhat a misnomer because Coriolis is not really a force; it's more a perception that occurs as a consequence of us living on a planet that is rotating.

- The Earth is a rotating platform. When viewed from above the North Pole, it rotates counterclockwise. A plane flying uncorrected from New York to Los Angeles will therefore appear to bend to the right as a result of this rotation. This deflection is called Coriolis.

- The Southern Hemisphere also experiences Coriolis, but instead it moves things to the left. This is because a counterclockwise rotation as viewed from the North Pole is the same as a clockwise rotation as viewed from the South Pole.

- Any wind (which is a movement of air) or current (which is a movement of water) can be influenced by Coriolis.

- There are many factors that can cause a current, but the content of this lecture will focus on 2: the wind and thermohaline circulation.

The Wind

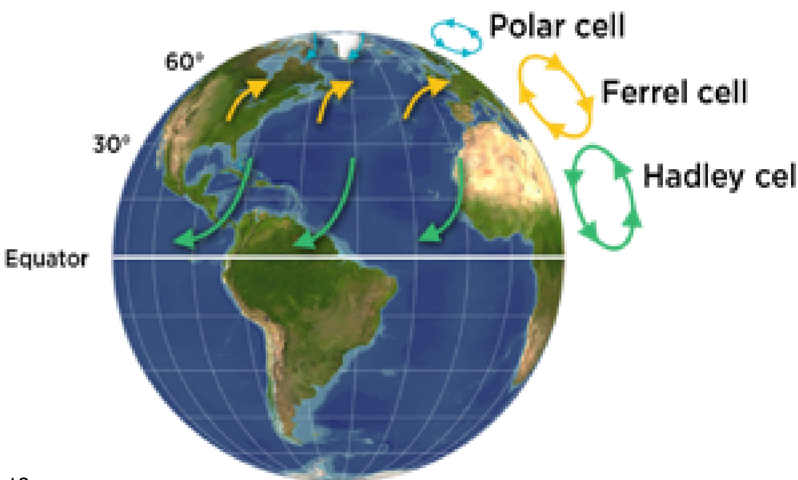
- The currents that most people are familiar with on a day-to-day basis are called wind-driven, or surface, currents. That is, the act of the wind driving along the surface of the water pulls some of the water with it in a shearing interaction. Thus, to understand wind-driven currents, we need to understand the wind, which is essentially a current of air.

◇ Winds at the scale of a planet are relatively easy to understand. Air moves from areas of high pressure to low pressure in an effort to equalize those 2 pressure zones. Differential pressure is caused by differential heating.

◇ Areas around the equator experience high amounts of radiation from the Sun. This is because the Sun, more or less directly overhead, is slicing through a relatively thin layer of atmosphere. Thus, the air at the equator is warm, and because that warm air is less dense, it will rise and start to spread north and south of the equator.

◇ As the air starts to cool, it will sink and eventually cycle back to the equator, where it is heated up again. This is called a circulation cell, and it is more or less predictable because the Sun heating the Earth in a particular way is more or less predictable.

◇ But we have yet to consider the impact of Coriolis in this model. Let's consider just the Northern Hemisphere. This first circulation cell, located just north of the equator and extending to about 30° north, is called the Hadley cell, named after a British amateur meteorologist.



- Return of air to the equator along the surface would be from the north to the south. However, Coriolis dictates that this movement would be deflected to its right. Therefore, the resultant wind moves diagonally from the northeast to the southwest. Remembering that we name winds for where they are blowing from, this means that we associate the northern Hadley cell as having predictable, consistent northeasterly winds and call them the northeasterly trade winds.

- The northern Hadley cell interacts with air just to the north of it, causing a second circulation cell called the Ferrel cell, named after an American meteorologist. This second cell extends to about 60° north, and it interlocks with the lower-latitude Hadley cell like gear cogs in a machine. So, in this cell, air rises at around 60° north, travels at altitude south until it converges with the Hadley cell, sinks to the planet's surface, and then travels along the surface from south to north to complete the circulation loop.

- But in the Northern Hemisphere, Coriolis force causes a deflection to the right, so instead we see winds traveling from the southwest-ish to the northeast-ish. Thus, the prevailing surface winds in the Ferrel cell are either westerlies or southwesterlies.

THE DUAL MEANING OF TRADE WINDS

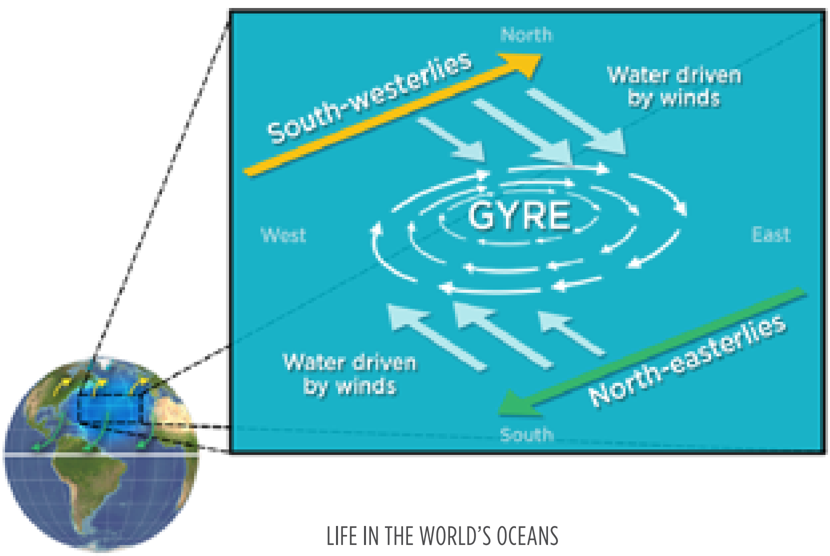
When it comes to trade winds, the word "trade" originally meant "path" or "track." And the phrase "blow trade" meant that winds were blowing along a constant, steady track—that is, they blew from the same direction in a predictable manner.

Later, however, etymologists incorrectly also associated the word "trade" with commerce, so we came to associate trade winds with those winds that would push boats from Europe to the Americas—in other words, from the northeast to the southwest—for the purposes of trade.

- The final circulation cell, the Polar cell, is located from 60° north and upward. It's a much narrower cell, and to interlock with the Ferrel, it circulates in the same fashion as the Hadley cell, with winds moving from the pole south along the surface. Coriolis force deflects these to their right, causing easterly winds because that particular circulation cell is so narrow.

- The cells that have been described for the Northern Hemisphere are mirrored in the Southern Hemisphere, so there is a southern Hadley, Ferrel, and Polar cell, resulting in surface winds that are, respectively, southeasterly, westerly, and easterly.

- Surface water is dragged by these surface winds in directions that are more or less parallel to the wind. So, if we were to look at the North Atlantic basin, we can imagine a southwesterly wind traveling along the top northeastern edge and a northeasterly wind traveling along the bottom southwesterly edge. Those 2 winds pulling along water will eventually cause a circular current called a gyre that in that basin is clockwise.



- Because these winds are predictable in both Southern and Northern Hemispheres at these different latitudes, we end up with 2 clockwise gyres in each of the North Atlantic and North Pacific Oceans and 3 counterclockwise gyres in the South Atlantic and South Pacific oceans, as well as the Indian Ocean.

- In contrast to the winds, we name currents for the direction in which they are traveling. So, a northerly current is moving from the south to the north (as compared to a northerly wind, which is moving from the north to the south).

The Thermohaline Current

- Surface, or wind-driven, currents play an incredibly important role in understanding the oceanography of our planet. These kinds of currents can deliver materials from nutrient-rich areas to nutrient-poor areas, thus infusing them with the potential for life. Currents can also have specific effects on local weather. While these kinds of currents can be locally important, of much more profound significance is a second kind of current: the thermohaline current.

- Most people will never see a thermohaline current because they happen deep underwater, in the abyssal depths of our oceans. But they are profoundly important because they regulate the heat balance of our planet. Therefore, we feel their effect every day.

- Water has a high specific heat capacity, meaning that it can absorb heat without changing too much in temperature. And heating of Earth's surface is uneven, with much more radiation received at the equator than at the poles. This heat is redistributed partly through air movement, but also through the movement of water cycling through the ocean's depths.

- In these kinds of currents, the poles are incredibly important. In brief, both the North and South Poles are surrounded by water that is constantly being cooled. Cold water becomes dense and therefore sinks, spreading out from high latitudes toward low latitudes. The water that has sunk has to be replaced with more water from the surface, which indirectly comes from low latitudes. A cycle is created, redistributing heat across the entire ocean.

- The name of this process is thermohaline circulation, but one of the circuits that is created also has a more common name: the global ocean conveyor. This circulatory system plays an unmatched role in regulating the planet's climate.

- You might recall from your geography lessons that from a bird's-eye view, there are essentially 7 oceans: the North and South Pacific, the North and South Atlantic, the Indian Ocean, the Southern Ocean, and the Arctic Ocean. But if you look carefully at any global map, you will notice that all of these oceans are connected.

- Perhaps we only have one ocean filling into several basins. If you look at in this way, you will start to notice that there is much more water on this planet than there is land.

- How does all the water in these basins interact and interchange? To understand this, we have to leave our bird's-eye view and think in a more 3-dimensional sense. What does the density structure look like as we move vertically down through the water column? The answer is that it depends on where you are.

It is ironic that we decided to call our planet Earth, because in reality there is much more water at the surface than there is earth.

- The density of seawater is quite variable. The 3 major factors that control density are temperature, salinity, and pressure, although pressure plays an almost negligible role because water is essentially incompressible.

- However, if you are in hot areas, where there is more evaporation than there is precipitation, the water will increase in salinity and therefore become denser.

- Paradoxically, in areas where it is cold enough to freeze water, you can also create saltier water because salt is often excluded when the ice lattice forms, a process called brine rejection. Again, this would cause the water immediately below the ice to become denser.

- In both of these cases, that denser water will tend to sink, until a point that it reaches its neutral buoyancy—that is, a point when that water has the same mass as the water surrounding it for a given volume.

- Similarly, water that is cooled, perhaps because it is in the higher latitudes closer to the poles, will become denser and therefore will sink.

- The act of water sinking because of its increased density is a movement of water, and therefore a current. These currents are called thermohaline because the sinking is due changes in temperature ("thermo-") and salinity ("-haline").

- You might imagine that this process of creation of more dense water is fairly common toward the poles, where water is both being cooled and there is the potential for brine rejection. The sinking water has an associated density signature, as represented by specific temperature and salinity values; in fact, we might refer to its TS signature, and we would refer to the parcel of water that is sinking as a water mass.

- ◇ Water masses are huge, vast volumes of water that are constantly being generated at their source and sinking to their point of neutral buoyancy, if they ever reach one. In this movement, they create circuits of moving cold water that is then replaced by warmer water. This is the essential idea behind the global ocean conveyor.

- ◇ Water masses often stack up on top of each other according to their density. The interface between 2 water masses is called a front, and it represents a rapid change in density condition, and therefore water quality. This front is directly analogous to the fronts that weather forecasters talk about; in their case, they are referring to an interface between 2 air masses, also of differing density.

LECTURE SUPPLEMENTS

Readings

McIntyre, ed., *Life in the World's Oceans.*

Vallis, *Climate and Oceans.*

Worsley, *Endurance.*

Web Resource

Smithsonian Institution, "Ocean Portal: Planet Ocean," http://ocean.si.edu/planet-ocean.

Questions to Consider

1. What is the prevailing wind direction where you live? Given the atmospheric circulation discussed in this lecture, in which circulation cell are you? If you live by the ocean, what is the dominant current? Can you predict its direction given the circulation cell in which you live? If not, what local processes are changing that prediction?

2. If you live on the coast, what water masses lie closest to where you live?

3. Using your own research, discover how long it takes for a parcel of water to make one complete loop of the ocean conveyor.

3

THE ORIGIN AND DIVERSITY OF OCEAN LIFE

In 1952, Stanley Miller and Harold Urey created a chemical soup of basic compounds believed to be abundant in primordial, prelife Earth, including water, ammonia, methane, and hydrogen; they heated this soup in the absence of oxygen. Then, they fired electrical sparks through the gaseous mixture to simulate lightning. After a week, organic compounds had arisen spontaneously from inorganic raw materials. Urey and Miller's historic experiment now represents an important step in our quest to understand the origin of life, and this lecture will focus on how we believe life evolved in the ocean.

The Development of Life

- In a broad sense, there are 3 common theories as to how life developed on this planet.

    1. Creationism. What we have learned about evolution and the age of the Earth for the most part speaks against common creation theory.

    2. Panspermia. This theory suggests that either actual life, in the form of bacteria, or just the complex building blocks for life exists throughout the universe and somehow hitchhiked its way to our planet on various asteroids and comets. Again, there is very little evidence to support the idea of panspermia.

    3. Abiogenesis. The most scientifically plausible theory of the origin of life is the spontaneous origin theory, or abiogenesis, the nonbiological process of life arising from nonliving matter. We believe that the origin of the universe—the event referred to as the big bang—probably occurred less than 14 billion years ago. Earth formed around 4.5 billion years ago, and the first primitive life probably emerged around 4 billion years ago.

- The early atmosphere of Earth was free of oxygen, but there were plenty of other simple molecules that could become the building blocks of life. Urey and Miller's experiment was so important because it proved that the complex organic molecules that are so essential to life could be formed from simple inorganic molecules, such as hydrogen and methane. All that was required was a suitable energy source—in this case, modeled lightning.

- The definition of life is somewhat complex and controversial. But chemically, most cells that we would define as alive contain 4 essential organic polymers: carbohydrates, fats, proteins, and nucleic acids. Each of these highly complex chemicals is made up of simple monomers—respectively, monosaccharides, fatty acids, amino acids, and nucleotides.

- Urey and Miller's experiment, and its kin, suggested that the formation of these organic building blocks and their subsequent polymerization to more complex forms would happen in the atmosphere where lightning would be available. The resultant complex molecules would then precipitate out onto the ocean, explaining the origin of life in the world's oceans.

- However, in 1977, a very interesting alternative environment was discovered. Diving deep in the Galapagos Rift in the Pacific Ocean, the crew of the now-famous submersible *Alvin* discovered vents in the ocean floor pouring thick black fluid into the water. As it cooled in contact with the cold water, this fluid would solidify into casings that created volcano-like tubes. These strange formations were originally called black smokers; they are now known as hydrothermal vents.

- Hydrothermal vents tend to be associated with volcanic activity. However, hydrothermal vents are not spewing lava; instead, they are actually very similar to land-based geysers, such as Old Faithful in Yellowstone National Park.

- Careful analysis of the effluent in a hydrothermal vent demonstrates that it is superheated water—water that has seeped down through cracks in the seafloor common around submarine volcanoes. Hydrothermal vents possibly play an important role in abiogenesis because the superheated water might have done

Hydrothermal vents are very similar to land-based geysers.

what the electrical sparks did in the Miller and Urey experiment: It may have provided a source of energy to start the conversion of simple inorganic compounds to more complex organic ones.

- As if to support this idea, hydrothermal vents support densely populated ecosystems that are highly localized. It is as if the hydrothermal vent is acting as an oasis, attracting life on an otherwise featureless abyssal plain.

- But at these depths, the ocean is pitch black. How can such organisms live so far away from the photosynthetic producers that would normally be at the base of their food chain? The answer is that life has found a way.

- Certain bacteria use a process called chemosynthesis, drawing energy not from the Sun but from various sulfide compounds present in the smoker's effluent. This energy is then used to form carbohydrates and other important organic compounds necessary for life. These bacteria act as the base of a food web in place of photosynthetic life, providing energy that either directly or indirectly sustains all the organisms around the vent.

- Extremophiles are a hot topic of research for those interested in abiogenesis because they can live in extreme conditions similar to those experienced in a primordial, prelife Earth, and they catalyze or mimic some of the reactions we believe would have been necessary to abiogenesis.

Giant tube worms (*Riftia pachyptila*) have no digestive tract. Instead, chemosynthetic bacteria in the worms' bodies draw energy from hydrothermal vents and convert it into organic matter that nourishes the worms.

- There are a lot of missing links in the abiogenesis story. For example, how did evolution move from the formation of various complex organic polymers in the primeval environment to the formation of the nucleotide-based compound RNA, from which we believe life began? And how did the cell evolve? We still don't have good answers to either of these questions, but perhaps in our lifetime we will.

The Classification of Living Things

- Carl von Linné, the Swedish naturalist who was better known as Carl Linnaeus, created the hierarchical classification scheme with which most people are familiar today. According to Linnaeus, the natural world could be organized into 3 fundamental kingdoms: plants, animals, and minerals. He developed a system of hierarchies that, with some modification, has become the classification system we use today.

- That system, known as the Linnaean system, starts with kingdoms and then goes on to phyla (or divisions, for plants), classes, orders, families, genera, and species. We typically refer to a species by just its genus and species name—for example, *Megaptera novaeangliae* (humpback whale).

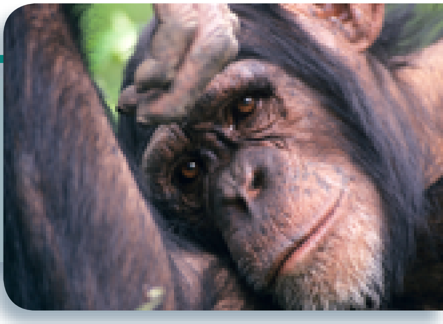
- As an 18th-century naturalist, Linnaeus did incredibly well, using only his remarkable powers of observation to parse out life into the various kingdoms.

KINGDOM
↓
PHYLUM
↓
CLASS
↓
ORDER
↓
FAMILY
↓
GENUS
↓
SPECIES

◇ However, with the dawn of the molecular age 200 years later, we began to develop the ability to compare genetic codes between species. In other words, genetic codes that were similar implied a high degree of relatedness.

OUR CLOSEST RELATIVES

Depending on which subset of genes you look at, chimpanzees and humans share about 98% of their DNA. We are therefore more closely related to chimps than to, for example, giraffes.



◇ With the advent of this technology, we have been able to review the Linnaean system, and 2 trends have emerged: that a few tweaks have been deemed necessary and that by far the greatest molecular diversity found in any group occurs in the bacteria.

◇ After Linnaeus, new kingdoms were added to his basic scheme. And for a while, all bacteria were grouped together in a kingdom called Monera. But this turns out to be a gross oversimplification. To fully capture the diversity of life on Earth, we needed to add a whole new fundamental division above kingdoms, called the domain.

◇ There are 3 domains. Two of them, the Archaea and Bacteria, are devoted to the entire former kingdom of Monera. A third domain, Eukarya, contains everything else, including the remaining 4 kingdoms. In terms of classification, 3 of those 4 kingdoms seem on fairly solid ground: Animalia, Plantae, and Fungi. Protista, the group that contains organisms such as the amoeba, is still under review.

◇ Even though bacteria are tiny, single-celled organisms, they are unarguably the most successful organisms on this planet. Bacteria can act as producers; many are photosynthetic. They can also be at the base of chemosynthetic food chains. They have symbiotic relationships with many organisms, allowing hosts to do so much more because the bacteria specialize in certain chemical reactions. In addition, bacteria have exploited pretty much every niche available on this planet. And in spite of their small size, their biomass likely exceeds that of all other organisms put together on this planet.

IDENTITY CRISIS

You're human. You're made of approximately 30 trillion "human" cells. Yet there are also 40 trillion bacterial cells living in your body—some as pathogens, some as symbionts. So, are you more *you* than bacteria, or vice versa?

The Diversity of Life in the Ocean

◇ Bacteria play an indispensable role in the marine ecosystem. Some act as primary producers in either chemosynthetic or photosynthetic-based ecosystems; some act as decomposers, returning complex organisms back to simple chemical compounds that then become the nutrients needed for future life. They have been found in all parts of the ocean, including the frigid polar oceans and the roasting-hot black smokers.

◇ All bacteria have a prokaryotic design—a particularly important fact that contributes to their success. Relatively, prokaryotes are fairly basically designed. Consisting of only one cell, the interior of a prokaryote is simple; there is no nucleus. This

simple design makes replication through cell division much more straightforward. In essence, this means that bacteria can reproduce very quickly. Bacteria can also adapt to changing environmental conditions very quickly—another reason for their extraordinary success.

- ◇ The remaining domain in our classification scheme is Eukarya, so named because their cellular organization is eukaryotic rather than prokaryotic. Eukaryotic cells are considerably bigger than prokaryotic cells. The nucleus is one of many organelles inside a eukaryotic cell that can usually be easily seen with the aid of a microscope.

DOMAIN	KINGDOM	CELL TYPE
Bacteria	Eubacteria	Prokaryote
Archaea	Archaebacteria	Prokaryote
Eukarya	Protista Fungi Plantae Animalia	Eukaryote

- ◇ Because they possess organelles, eukaryotes can compartmentalize metabolic activity and confine it to certain parts of the cell. However, such complexity makes reproduction more complex, so eukaryotes cannot divide as quickly as prokaryotes.

- There are millions and millions of marine-based single-celled eukaryotic organisms in our oceans. Traditionally, these all would have been put in the kingdom Protista, but that kingdom now appears to be more a catchall of convenience rather than a true taxonomic classification.

- Only so much can be achieved as a single-celled organism. With multicellularity comes the ability to organize and delegate organismal functionality at the level of tissues, organs, and organ systems. So, life has also evolved into an array of eukaryotic multicellular forms.

- There are 3 multicellular kingdoms: Animalia, Plantae, and Fungi, which have variable distributions in the marine environment. For example, marine fungi are much less successful and diverse than their terrestrial counterparts, although they play much the same ecological function in an ecosystem—for the most part as decomposers and in some cases as pathogens.

- Kingdom Plantae is represented in the marine world in several important ways. This group now includes the red and green algae. In fact, the ancestor of all land plants is believed to have derived from an organism very similar to a chlorophyte, which is the informal name for Chlorophyta, the phylum name for green algae.

- However, there are relatively few examples of vascular plants that are exclusively marine. There are plenty of examples that live on the boundary between the marine and terrestrial environments—for example, mangroves, dune grasses, and various species found in salt marshes. However, only the seagrasses are completely marine, comprising 4 families that live in the seabeds of shallow areas, where there is enough light to make photosynthesis possible.

- That leaves us with the final kingdom, Animalia. Most animal species on this planet are invertebrate, and therefore most marine animal species are also invertebrate. All animals are heterotrophs; they must feed to obtain calorific energy. However, the ways in which animals feed is extremely diverse. Also, although most animals are mobile at some point of their life history, many have significant sessile stages, meaning that they are fixed in one place during these stages. Within the invertebrates, many species have a planktonic phase that aids in their dispersal. Such animals are called zooplankton.

- The various marine phyla that fall under the kingdom Animalia include Porifera, or sponges; Cnidaria, including planktonic jellyfish, sessile sea anemones, and various coral polyps; Ctenophora, or comb jellies; Platyhelminthes, or flatworms; Nematoda, or roundworms; Annelida, or segmented worms; Mollusca, including bivalves (for example, clams, oysters, and scallops), gastropods (or marine snails), and cephalopods (including squid and octopus); Arthropoda, including horseshoe crabs and crustaceans (including crabs, lobster, and shrimp); Echinodermata, including sea stars, brittle stars, sea urchins, and sea cucumbers; and Chordata, including fish, reptiles, birds, and mammals.


Octopus vulgaris

LECTURE SUPPLEMENTS

Readings

Amaral-Zettler, Artigas, Baross, Bharathi, Boetius, Chandramohan, Herndl, Kogure, Neal, Pedrós-Alió, Ramette, Schouten, Stal, Thessen, de Leeuw, and Sogin, "A Global Census of Marine Microbes."

Margulis and Dolan, *Early Life*.

Margulis and Sagan, *What Is Life?*

Questions to Consider

1. Urey and Miller's original experiments were pioneering, but what other significant experiments have occurred to help us understand the origin of life? (Search the Internet for names such as Alexander Oparin, Robert Shapiro, Sidney Fox, Sol Spiegelman, and Craig Venter.)

2. Review the principles of Linnaean homology and analogy and how they might be used to develop a system of taxonomy.

3. Research the main differences between prokaryotic and eukaryotic life. Which do you think is the more "successful" form? How are you defining "successful"?

4

BEACHES, ESTUARIES, AND CORAL REEFS

In this lecture, you will learn about 3 important types of highly specialized environments that are found in the ocean: beaches, estuaries, and coral reefs. In examining each of these 3 environments both physically and biologically, you will gain a better understanding of the role they play in the world's ocean.

Beaches

- Beaches represent an interface between land and sea, and they can be highly varied in their morphology, typically as a function of the prevailing wind and wave energy. Some beaches directly face the open ocean and therefore will be exposed. Others will be tucked away at the back of estuaries; lagoons; or long, convoluted bays and therefore are more sheltered.

- In areas that are extremely exposed, there is a high amount of wave energy. This will often act to keep finer sediments in suspension; every time they try to settle, they will once again be lifted up into suspension. So, the only material that stays on the beach tends to be the larger particles—for example, cobbles, gravel, and boulders.

- High-energy beaches tend to be steeper because the sediments from which they are made tend to be of a larger diameter, and such particles are much easier to stack. Think about the differences in pore size between a sand and a cobble beach—or, in other words, the spaces between grains. There's much more space between particles of a steep beach because the particles are larger.

- With a high-energy beach, this is a good thing. Tall waves delivering tons of water onto the land can have a significant erosive effect. However, the large pores between sediment particles on a high-energy beach allow a substantial portion of the water from those waves to percolate down and back out to sea. Thus, the profile of the beach can be maintained.

- Low-energy beaches tend to be shallower in angle and are made of finer grains of sediment, such as sand or even mud. This is because the low energy allows smaller particle sizes to settle without being resuspended into the water column or eroded. However, the relatively small interstitial pore size between sediment grains has 2 important consequences.

1 If unusually large waves hit such a beach, percolation is much reduced, and as a result, the beach gets eroded. One might also experience rip tides—sudden, instantaneous currents forcing their way back offshore because too much water has piled up on land.

2 Because there is not much water between particles, there is also not much dissolved oxygen. This can often lead to an anoxic environment, one free of oxygen. Beaches made of mud or silt are often quite odorous, having the smell of rotten eggs. This is because of bacteria living in the sediment that have found a way to exist without the presence of oxygen. Instead, they use alterative chemical pathways that result in the production of hydrogen sulfide, the gas responsible for that smell.

- The beach changes shape over the course of the year. This is because wave energy has a seasonality that is associated with storm activity. Creatures that live in that environment must deal with the fact that the beach is a highly dynamic environment.

- Because a beach is on the interface between land and sea, it also experiences tide, which is the effect seen when 2 astronomical bodies—the Sun and the Moon—pull on Earth's water. Depending on where you live on the coast, you might experience a diurnal or semidiurnal tide. Diurnal tides result in one high and one low tide per day. Semidiurnal tides have 2 highs and 2 lows per day. The vertical distance between the low and high tide is referred to as the tidal range.

- Throughout a lunar cycle, the tidal range varies; in other words, the vertical difference between the high tide and the low tide changes as the Moon waxes and wanes. The range is largest when the effects of the Sun and the Moon combine constructively, making high tides higher and low tides lower. These are called spring tides, and they occur at new and full moons.

- The tide has its narrowest range during periods of half-moon, when the Sun and the Moon are pulling orthogonally to each other. These are called neap tides. Thus, every 28 days, there are 2 spring tides and 2 neap tides, and everything in between.

- The part of the beach that is exposed at low tide but submerged at high tide is referred to as the intertidal, or littoral, zone, which is populated by a group of flora and invertebrate fauna that are remarkable in their ability to cope with large swings in environmental conditions. The intertidal zone represents a pioneering front where organisms face the challenges of a terrestrial environment on a periodic basis.

- Depending on where you live in the world, the tidal range can be incredibly large or quite narrow.

- The horizontal extent of a tide depends on the slope of the beach. For a shallow beach, the tide might go out hundreds of meters, even though the tidal range is small. On a steep beach, the horizontal extent of the tide may only be about 50 meters, even though the tidal range is 4 meters.

- As an organism moves from sea to land, there are 2 principal challenges. First is the sudden absence of water. The minute an intertidal organism is uncovered, it risks desiccation, or drying out. The second challenge is the lack of physical support. In water, the body mass of the organism is supported. On land, gravity fully comes to bear, and the organism risks being crushed by its own weight. Thus, the position of an organism relative to the tidal range is of crucial importance to the survival of that organism.

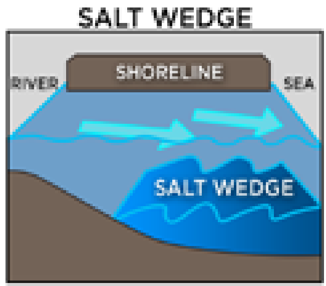
- There are a variety of challenges that face an evolving intertidal organism, so why is there pressure to leave the water in the first place? The answer is predation. The impact of predation marks the lower limit of how far an intertidal organism might range; too low and it risks exposure to marine-based predators. The upper limit is controlled by physical factors, such as length of emergence, desiccation risk, and competition with other organisms.

- In this way, the intertidal zone is often divided into belts of different communities of organisms; their position is a compromise between various evolutionary-based selective forces.

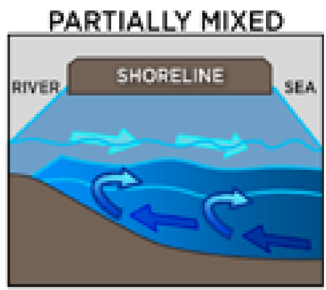
Estuaries

◇ Whereas beaches represent an interface between land and sea, estuaries are an interface between river and sea, a mixing of freshwater and saltwater. There are 3 basic kinds of estuary, depending on how strong the outflow of the river is in comparison to the strength of tidal input from the ocean.

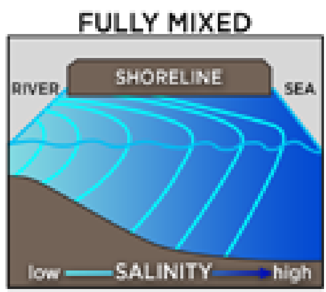
1. A salt-wedge estuary is one where the river dominates the system. There is very little mixing between freshwater and seawater, and the boundary between the 2 is marked by a sharp interface that represents a rapid change in salinity. This boundary is referred to as a halocline. The incoming ocean water, being denser, slides underneath the outgoing, less dense freshwater, as a wedge.



2. As tidal input becomes more dominant, the salt wedge and the outgoing freshwater start to mix, and the halocline becomes less sharp. This is the second kind of estuary, known as a partially mixed estuary.



3. As tidal forces dominate, we move to a fully mixed estuary. These often happen in very large river mouths—for example, the Chesapeake Bay.



- Estuaries again represent a challenging environment for many marine organisms, to the point that many predators typically cannot work in such areas. For this reason, many species, particularly fish, use estuaries as nursery areas. The challenge is to cope with the varying salinity conditions.

- A marine fish living in saltwater is living in a solution of salts that is at much higher concentration than the level of salts inside its body. This sets up a concentration, or osmotic gradient, whereby water wants to leave the body of the fish, a potentially dangerous condition. To counteract this, a marine fish has a number of adaptations to retain water.

- In contrast, a freshwater fish represents a body of salts living in an environment where the concentration of salt is very low. The concentration gradient that is set up now works in reverse; water tries to enter the fish, again a potentially dangerous condition if left unchecked. So, freshwater fish have a number of adaptations to help them lose water.

- Fish that live in a brackish, or estuarine, environment fall somewhere between these 2 extremes but may end up living in one of those 2 environments permanently once they become adults. So, they need adaptations to salinity that are at the very least variable.

- Estuaries are also very rich in invertebrates. Typically, invertebrates adopt another strategy known as osmotic conformation. Through a series of molecular level pumps, they match the salinity of their environment so that there is no gradient between organism and surrounding water. Therefore, water neither wants to move in or out of the organism.

- Estuaries are profoundly important to ocean productivity and are ecologically unique. They often have biodiverse and fragile salt marshes associated with them, and they can support thriving

populations of invertebrates and various wading birds. Some species of plant have adapted to the presence of salt, a condition known as halotolerance.

◇ Unfortunately, many estuaries are polluted because, after all, they represent the terminus of rivers into the ocean. Everything we dump in a river ends up there. Recently, there has been an environmentally inspired movement to clean up estuaries in many of the countries of the Western Hemisphere. If there is an estuary near you, find a local advocacy group and help with the cleanup and monitoring of it.

Egrets are one of many varieties of wading birds that thrive in estuaries.

Coral Reefs

- Loosely, corals can be divided into 2 groups—the soft and hard corals—although when most people think about coral, they are probably imagining the hard type. Soft corals tend to be found in deep water. Hard corals are found in shallower water and secrete a calcium carbonate exoskeleton to protect themselves from predators and wave action; this is because they like living in the highly oxygenated water close to the surface, but must suffer the impact of the waves as a result.

- There are 3 different types of coral reef structures: fringing reefs, barrier reefs, and atolls.

  1. A reef starts as a fringing reef, typically attached to a shoreline or an island. Such a reef will have 3 distinct parts: the reef flat, the reef crest, and the fore reef, which becomes the reef face or wall. If, over geological time, the water level rises or if the land subsides at a relatively slow rate, the reef will continue to grow upward even if the land around it has sunk.

  2. This results in a barrier reef—one that more or less surrounds an island, often with a calmer lagoon between the reef and the island. Lagoons are calm and secure areas that develop their own ecosystems.

  3. If sea level continues to rise, then the original landform in the center of a barrier reef may disappear completely, yet the reef will continue to grow upward. In this way, an atoll is formed, a ring of reef surrounding an open lagoon. Some atolls are very old and stand next to incredibly deep water.

- Key to this model is the assumption that reef growth can keep up with the rate of sea level rise or land subsidence. Sometimes it can't keep up, and the reef gets drowned.

- The value of reefs lies in their extraordinary biodiversity. They are the aquatic equivalents of rainforests. Nowhere else can you go in the world and discover so many species in so concentrated an area.

- Global climate change, including increased water temperatures and ocean acidification, can have dramatic impact on the reefs of the world. Higher temperatures may cause the disassociation of the polyps from the algae, causing the coral to lose its color, as well as an essential partner for the purposes of nutrition. This phenomenon is known as coral bleaching.

THE GREAT BARRIER REEF

The largest biologically built structure in the world is the Great Barrier Reef, a collection of more than 2900 individual reefs spanning a distance of more than 2300 kilometers.

Considered to have "outstanding universal value," the Great Barrier Reef was designated as a World Heritage Site by UNESCO in 1981.

However, scientists are now concerned about the future of the Great Barrier Reef. All reefs have both natural and unnatural predators. Crown-of-thorns sea stars are voracious predators of coral, and while they play an important regulatory role in a healthy reef, this species will cycle in abundance every 20 years or so. In outbreak years, the impact can be highly significant.

- Ocean acidification will not only prevent corals from harvesting calcium carbonate from the environment, but it will also cause an erosion of the already-built exoskeletons. These are important and serious problems that can only be solved globally. Reefs are also extremely susceptible to pollution.

LECTURE SUPPLEMENTS

Readings

Cole and Michael, *Reef Life*.

Knowlton, Brainard, Fisher, Moews, Plaisance, and Caley, "Coral Reef Biodiversity."

Martinez, *Marine Life of the North Atlantic*.

McCalman, *The Reef*.

Rosenfeld, *The Intertidal Wilderness*.

Web Resources

Smithsonian Institution, "Ocean Portal: Beaches," http://ocean.si.edu/ocean-life-ecosystems/beaches.

———, "Ocean Portal: Coral Reefs," http://ocean.si.edu/ocean-life-ecosystems/coral-reefs-0.

———, "Ocean Portal: Mangroves," http://ocean.si.edu/ocean-life-ecosystems/mangrove-forests.

Questions to Consider

1. Research the tidal cycle at your nearest marine beach. Is it diurnal or semidiurnal? What is the maximum tidal range (that is, during a spring tide). If you can visit that beach, perform a survey of the organisms you find in the intertidal area. Are there patterns of distribution, and can you make sense of those patterns knowing a little bit about the life history of those organisms?

2. In a flat bowl, stack pebbles in a pile as steep as you can manage and then pour water over them. In each case, look how the shape of the pile has changed. Do the same with a pile of sand. What does your experiment tell you about the stability of beaches, and their corresponding slopes, as a function of grain size?

3. Compare and contrast the productivity found in mangrove swamps versus coral reefs.

4. Should the Great Barrier Reef be considered one giant symbiotic organism?

5

LIFE IN POLAR AND DEEPWATER ENVIRONMENTS

In this lecture, you will learn about the polar ecosystems of the Arctic and the Antarctic. You will also examine the temperate areas of the ocean. While you might imagine colorful reefs in the tropics bathed in sunlight and teeming with life, in reality the productivity of tropical oceans pales in comparison with the potential productivity of the higher latitudes. The lecture will end with a brief examination of another type of ecosystem that is very far from the influence of the Sun: the abyssal depths.

Differences in Productivity

◇ The term "productivity" relates to photosynthetic and chemosynthetic activity of primary producers—chiefly single-celled algae and certain species of bacteria, collectively termed phytoplankton. These are the "grass" of the ocean, creating the food upon which the rest of the ecosystem is based.

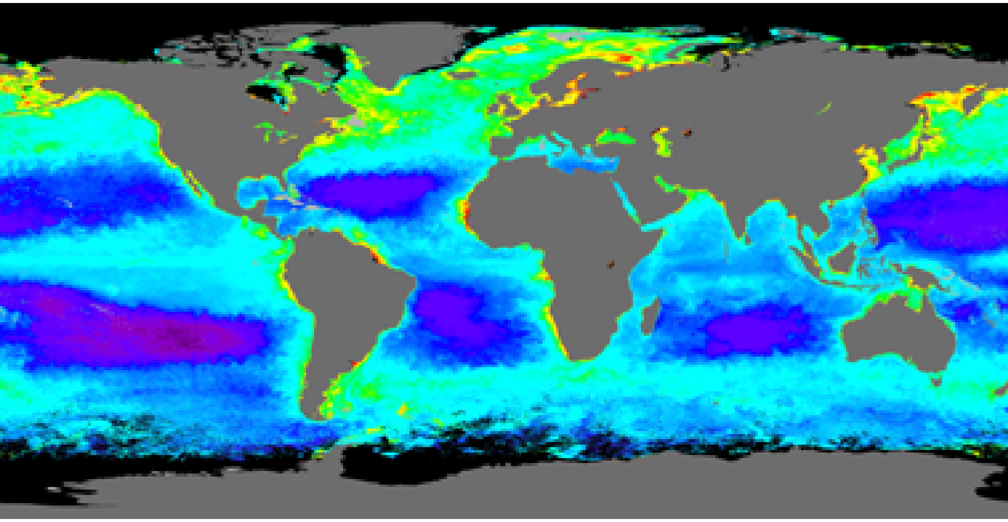
◇ We measure productivity in grams of carbon per meter squared per year, which determines the amount of sugar molecules that are created as a result of fixing carbon from carbon dioxide through either a chemosynthetic (in dysphotic and aphotic zones) or photosynthetic (in areas that have good access to light) process.

◇ Another proxy for photosynthetically based productivity is the concentration of a pigment known as chlorophyll *a* in the water, measured as milligrams of chlorophyll *a* per meter cubed. This number turns out to be strongly related to the density of phytoplankton in the water column.

◇ Chlorophyll *a* turns out to be reasonably easy to measure, because it colors our water slightly green, and we can calibrate satellites to look for that. In this way, we can get large, basin-scale assessments of primary productivity very quickly.

◇ Images taken by a satellite of photosynthetic productivity in the world's ocean show some clear trends.

1 There is seasonal variation, with peaks occurring in the Northern Hemisphere during the boreal spring and summer and in the Southern Hemisphere during the austral spring and summer. This makes sense because photosynthesis is linked to light availability, which is best during the spring and summer months.



2 There is higher productivity in shallow areas, such as continental shelves. This is because mixing processes in shallow areas allow nutrients to come to the surface and help feed the photosynthetic reaction.

3 There are large parts of open ocean and many tropical areas close to shore that are relatively poor in productivity. That is because open oceans typically lack focusing mechanisms to bring organisms together, and tropical areas tend to be nutrient limited because of ocean stratification.

4 In general, productivity rapidly improves past 40° north and south. In fact, in these latitudinal bands, there are even cases in the open ocean where there are high levels of productivity. Productivity is higher in temperate regions because of a unique combination of light and nutrient availability that creates both a spring and fall bloom of phytoplankton growth. A majority of the world's most important fisheries are, or were, in these areas. As one moves to even higher

latitudes, the potential for productivity gets even higher; however, we now move into a light-limited situation, so while productivity in polar regions is high for a few select months, for the rest of the year the photoperiod is too narrow to generate much phytoplankton growth.

Even though life in the tropics looks beautiful and is highly biodiverse—for example, coral reefs have been referred to as the rain forests of the ocean—by comparison of biomass, the tropics are deserts compared to what the temperate and polar zones can produce.

The Southern Ocean Ecosystem

- The Antarctic, or Southern, Ocean surrounds the continent of Antarctica, and the ecosystem it contains has a very real, oceanographically defined northern boundary: the Antarctic Convergence, or Polar Front. The convergence represents the interface between 2 water masses: the cold Antarctic Surface Water and the less cold Subantarctic Surface Water.

- The front circumscribes the continent of Antarctica and is found at different latitudes depending on the ocean basin: In the Atlantic and Indian Oceans, it is located around 50° south but rises to 63° south in the Drake Passage and 60° south in the Pacific Ocean.

- One should not think about this boundary as being static; it oscillates back and forth, depending on the strength of cold-water mass generation closer to the Antarctic continent. Also, the front is not knife-sharp. In reality, it occurs over tens of kilometers, and the amount of time you spend in the front is a function of the angle at which you cross it.

- There are no physical features marking the front. However, as with most fronts, one tends to see an aggregation of sea life—in this case, various seabirds, whales, seals, and sea lions—attracted to the prey that gathers there. Also, the colder water tends to drop the dew point of warmer air traveling with the warmer water mass, causing mist or fog. In spite of all this, still the best way to tell if you have crossed the convergence is to monitor the water temperature. As you cross the front, the temperature will drop about 5 to 10° Celsius.

- The seafloor below the Southern Ocean is for the most part very deep, averaging around 4000 meters until one approaches the Antarctic continent. The seafloor is punctuated with a series of ridges as shallow as 3000 meters and trenches as deep as 5500 meters.

- Most of Antarctica is surrounded by continental shelf of varying width. The surface area of the continent itself exceeds 13 million square kilometers, of which about 99% is covered by an enormous ice sheet that averages 2 kilometers in depth. This is where you will find 90% of all of Earth's ice.

- During the austral winter, the southerly parts of the ocean freeze and the ice sheet expands farther out from the continent. This type of ice is known as fast ice, and it increases the area of the continent by another 20 million square kilometers. In other words, during the winter, Antarctica more than doubles in size.

- In spite of all this ice, most of the continent is technically classified as desert, because there is now so little precipitation. The exception is the Antarctic Peninsula, which receives more snow than average and has a more maritime climate.

Northern edge of iceberg B-15A in the Ross Sea

- Glaciers that begin inland move outward to the ocean and there calve into icebergs, some of which are incredibly large. For example, in 2000, the Ross Sea ice shelf calved a tabular iceberg that was almost 300 kilometers long and almost 40 kilometers wide—larger than Delaware and Rhode Island put together.

- The pelagic ecosystem of the Southern Ocean is based around an important keystone zooplankton species, southern krill (*Euphausia superba*). Krill is a shrimp-like organism that is a type of crustacean found in the Arthropod phylum that is about 3 to 4 centimeters long.

- Keystone species are so named because of the belief that with their removal, the ecosystem collapses for lack of that vital link between higher and lower trophic levels. A substantial portion of the ecosystem either eats krill or eats something that eats krill.

By some estimates by weight, krill could be the most abundant animal on the planet.

- Krill act as the keystone for the Southern Ocean ecosystem. There are other zooplankton present, but krill dominate. Given its importance, some researchers are extremely concerned about the sustainability of krill fishing in the Southern Ocean, the yield from which, for the most part, becomes fish food in various aquaculture projects. If we destroy the krill population, much of the Southern Ocean food web will also collapse.

- Krill are herbivores, feeding mostly on vast fields of algae that live on the underside of sea ice. Researchers are concerned that climate change might be creating a reduction in sea ice and potentially impacting krill's ability to feed. Ice can also act as a microhabitat in which krill can hide from predators, so we should do all we can to preserve the ice by reducing the effects of climate change.

- Krill's predators include fish, whales, seals, sea lions, and penguins as well as other seabirds. The sheer abundance of all these other organisms also speaks to the amount of krill that is available in the ecosystem.

- In addition to humans being apex predators in the Southern Ocean, there are 2 natural marine mammal predators to be found here, too. The first of these is the leopard seal. While leopard seals can and do feed on krill, they can also feed higher up the food chain, taking penguins and even small seals. There are also at least 5 ecotypes of killer whale, each specializing on a different prey type.

- We are slowly learning more and more about the Southern Ocean system as our technology becomes more advanced, allowing us to look at systems simultaneously at larger and larger scales. We also have treaties and conventions in place that encourage us to investigate these areas and develop sustainable management.

The crabeater seal focuses heavily on krill as a main part of its diet. In fact, the crabeater's dentition is specifically designed to take krill. By having a set of interlocking teeth, this species can take a krill-heavy gulp of water and filter the water out of its mouth by pushing it out through the gaps in its teeth, leaving the krill on the inside.

The Abyssal Plain of the Deep Ocean

- An area that we know very little about is the abyssal plain of the deep ocean. This ocean province accounts for more than 50% of the Earth's surface and is located between 3000 and 6000 meters in depth.

- The seafloor for the most part is covered with sediments that have rained down from above. These include red clays as well as carbonaceous and siliceous oozes, the remnant shells and tests of planktonic life-forms that sank to the depths after the organism's death.

- Superficially, the abyssal plain appears dead. However, the secret is in the infauna and inflora—organisms that live in the sediment. Recent surveys have demonstrated that the inflora and infauna of the abyssal sediments are much more biodiverse than previously suspected, including thousands of species of bacteria, various protozoans, and invertebrate species. Many of the species are previously undiscovered.

- Because of the complete absence of light, productivity in the abyssal plain must be chemosynthetically based. Chemosynthesis is a metabolic process within the exclusive domain of the bacteria, highlighting their importance at these great depths. Thus, bacteria, rather than phytoplankton, are at the base of the abyssal food chain.

- A number of fish and squids also live at these depths; where there is no light, these organisms often use their own light, a phenomenon known as bioluminescence. In some cases, this is done by bacteria, often ingested by the organism; in other cases, the organism itself generates the light.

- The colors produced by bioluminescent organisms are remarkable and serve a variety of functions, including camouflage, defense, and communication. One particularly cunning group of predators known as dragonfish illuminate their vicinity with a red light that cannot be detected by its prey because the prey simply do not have sensitivity to that wavelength of light.

- Our understanding of the abyssal depths will improve as technology permits. We continue to design both manned and unmanned submersibles that can sample at those depths as well as observe that ecosystem remotely. The vast expanse of the abyssal plain, coupled with the extremely hostile ambient pressures, will keep this ocean province very much a mystery for many years to come.

LECTURE SUPPLEMENTS

Readings

Baker, Ramirez-Llodra, Tyler, German, Boetius, Cordes, Dubilier, Fisher, Levin, Metaxas, Rowden, Santos, Shank, Van Dover, Young, and Warén, "Biogeography, Ecology, and Vulnerability of Chemosynthetic Ecosystems in the Deep Sea."

Coslow, *The Silent Deep*.

Ebbe, Billett, Brandt, Ellingsen, Glover, Keller, Malyutina, Arbizu, Molodtsova, Rex, Smith, and Tselepides, "Diversity of Abyssal Marine Life."

Gradinger, Bluhm, Hopcroft, Bebruk, Kosobokova, Sirenko, and Węslaswski, "Marine Life in the Arctic."

Gutt, Hosie, and Stoddart, "Marine Life in the Antarctic."

Hansom and Gordon, *Antarctic Environments and Resources*.

Jackson, Alexander, and Sala, eds., *Shifting Baselines*.

Matthiessen and Bateman, *End of the Earth*.

Nouvian, *The Deep*.

O'Reilly, *The Technocratic Antarctic*.

Secretariat of the Antarctic Treaty, "The Antarctic Treaty."

Van Dover, *The Ecology of Deep Sea Hydrothermal Vents*.

Web Resources

Commission for the Conservation of Antarctic Marine Living Resources, https://www.ccamlr.org/.

Marine Stewardship Council, https://www.msc.org.

Smithsonian Institution, "Ocean Portal: Poles," http://ocean.si.edu/ocean-life-ecosystems/poles.

Questions to Consider

1. Starting with changes in ice conditions and working through phytoplankton and krill availability, draw a flow diagram that shows how penguin species in the Southern Ocean may have been affected by climate change.

2. Investigate why certain Chilean sea bass (also known as Patagonian toothfish) are certified as sustainable and others are not.

3. What is the difference between photosynthesis and chemosynthesis?

6

PHYTOPLANKTON AND OTHER AUTOTROPHS

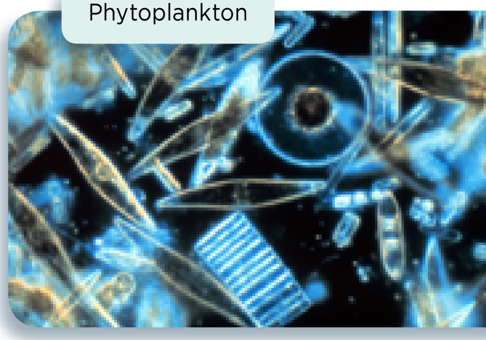
Plankton is essential to our oceans. Plankton forms the base of the food web upon which all marine life depends. The word “plankton” comes from the Greek *planktos*, which means drifter. This is a reference to the fact that plankton do not have the ability to move significant distances horizontally in the ocean and therefore rely on ocean currents to push them around. That said, many plankton species do have the ability to migrate up and down the water column.

Plankton

- Plankton can be broadly divided into 2 groups: phytoplankton and zooplankton.

    - The prefix "phyto-" means plantlike, and this is a reference to the fact that, similar to plants, phytoplankton have the ability to photosynthesize. Phytoplankton include many species of algae but in particular are dominated by diatoms, dinoflagellates, and many prokaryotic species. Among that last group are the cyanobacteria, which still get called the blue-green algae—even though, as prokaryotes, they are not technically algae.

    - In the term "zooplankton," the "zoo-" refers to animallike. The majority of zooplankton do, in fact, come from phyla within the kingdom Animalia. However, some are from a group known as Protista and therefore are not technically animals.



Phytoplankton

- Phytoplankton are autotrophs, and zooplankton are heterotrophs.

    - The term "autotroph" means self-feeding, and it is a reference to the fact that all autotrophs are capable of some kind of synthesis—that is, conversion of carbon dioxide in the presence of water to sugar molecules using energy harnessed either from the Sun (photosynthesis) or from other chemicals (chemosynthesis). While it is true that all phytoplankton are autotrophs, the converse is not true; in the ocean, not all autotrophs are phytoplankton.

◊ In general, heterotrophs do not have the ability to produce their own food (one exception is the mixotrophs, which are both heterotrophs and autotrophs at the same time). Heterotrophs must feed on other things to obtain calorific energy; the term "heterotrophy" means to feed on others. To do this, they can either feed on other heterotrophs or on autotrophs. Thus, as heterotrophs, zooplankton are by definition located higher up the food web than phytoplankton.

Zooplankton

The Marine Food Web

◇ Producers, or autotrophs, are at the base of the food web. They represent what we would call the first trophic level. The second trophic level, or primary consumer level, is occupied by what technically must be heterotrophic herbivores, because they are feeding on phytoplankton. The third level, or secondary consumer level, is occupied by heterotrophic carnivores—as is the fourth, fifth, and so on until we get to the apex predator, which in the marine world is usually a large fish or marine mammal, or perhaps a seabird.

◇ Don't get too hung up on the numerical value of these levels. In reality, a predator can feed across many trophic levels. What is more important is that mapping out predator-prey relationships in this way helps create a trophically dynamic system so that we can understand the interplay between organisms.

◇ Organisms at each trophic level do not necessarily have to be consumed by the predators at the next trophic level. They can also die naturally. In this case, the dead organism can be broken down by bacterial action. From a chemical point of view, this is taking the various complex organic molecules that represent the organism in life and breaking them down into simpler products. These products can then be reused by autotrophs as they continue to synthesize.

◇ Oceanographic mechanisms are important in delivering those simpler products, or nutrients, to areas where autotrophs can make use of them. In this way, phytoplankton are not homogenously distributed across the ocean. Rather, their distribution is heterogenous, organized around upwellings and other oceanographic focusing mechanisms.

◇ Thus, we can think of a food web not just as a linear, one-directional movement of organic molecules, but rather a cycling. Each trophic level plays an important role in transferring that energy to the next level. In marine ecosystems, both the phytoplankton and zooplankton play an essential role in that regard. As humans, we tend to place value on organisms at the top of food webs, but in reality, those organisms are ecologically no more important than organisms at other trophic levels.

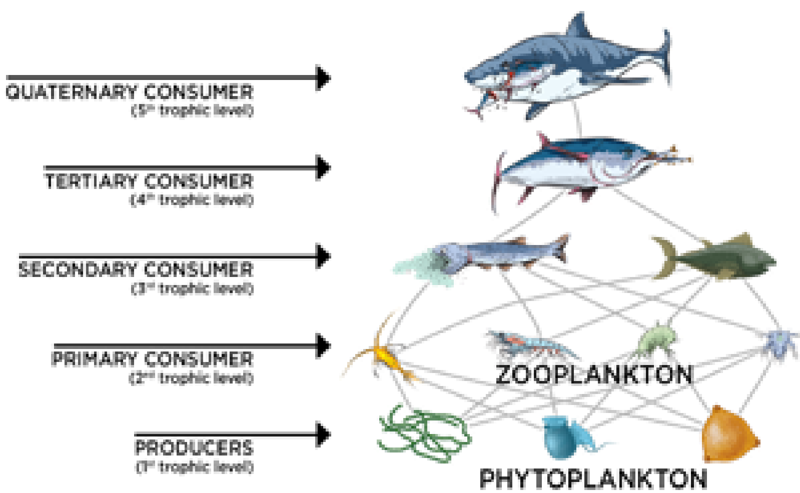
◇ At the base of the marine food web are phytoplankton, a majority of which are algae, protists, or prokaryotes. The algae fall into 2 kingdoms: Red and green algae have recently been reclassified as plants, so we find them in the Plantae kingdom as 2 separate divisions. However, there are also several important Protist phyla represented in the phytoplankton, as well as a phylum of bacteria.

◇ There are representative red and green, both single-celled and multicellular, algae that would be considered part of the phytoplankton. Green algae, also known as chlorophytes, are interesting because many believe they are the ancestors of

modern-day terrestrial plants. Most green algae are freshwater species, but a significant proportion are marine. However, there are relatively few red algae, or rhodophytes, that are single-celled and planktonic in their mature form.

◇ Both green algae and red algae are also commonly found in the intertidal zone in multicellular forms we call seaweeds. Because most seaweeds are attached to substrates within the intertidal, they are technically not plankton until they become unattached and start floating around at the mercy of local currents. There is, however, at least one form of free-floating seaweed that is technically planktonic: Sargassum weed, which lives exclusively in the Sargasso Sea, trapped by the North Atlantic gyre.

◇ That said, all seaweeds reproduce using motile gametes and disperse using spores. These stages in life history certainly would be planktonic. The slub on the underside of a boat, or the slime on a mooring buoy, are for the most part multicellular algal forms that have been dispersed planktonically.



- The majority of the single-celled eukaryotic phytoplankton in the ocean comes from 2 specific protist groups. The first of these are the diatoms, which belong to the phylum Heterokontophyta. Heterokonts are a very broad protist group that also includes the golden algae and the brown algae.

- Diatoms are incredibly abundant. A drop of surface seawater from pretty much anywhere around the world will contain some diatoms. They are extraordinarily beautiful in their external design; they possess silica-based walls called frustules that can be architecturally very complex and ornate.

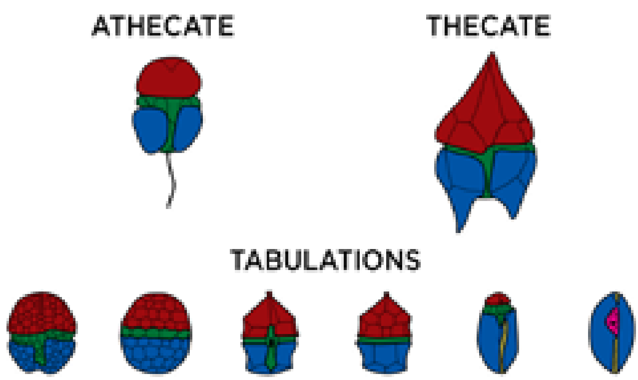
- Diatoms can be broadly divided into 2 orders: the Centrales, which have a round, radially symmetrical form; and the Pennales, which are bilaterally symmetrical and have a pennate form. Photosynthetic pigments give diatoms a yellow-brown color.

Diatoms are very common. It is thought that there may be as many as 100,000 different species, many of them currently undiscovered.

- Importantly, diatoms are not capable of individual locomotion in their mature form. Some use certain types of lipids that keep the cell more or less neutrally buoyant. Otherwise, they must rely on upwelling ocean currents to keep them at the surface. A diatom that sinks into the dysphotic and aphotic zones dies and quickly becomes part of what is called marine snow, a generic term given to the sinking of organic and inorganic particles through the water column to the seafloor. Marine snow is a major transportation pathway to deliver nutrients to greater depths.

- The second protist group is the phylum Dinoflagellata. The name, from Greek and Latin roots, means whirling whip, a reference to the 2 whiplike flagella that work to provide the cell with a weak twirling motion. This limited mobility is probably important in keeping a dinoflagellate close to the surface and therefore within the photic zone.

- Dinoflagellates can be divided into the thecate, or armored dinoflagellates, and the athecate dinoflagellates. The theca is similar to the diatom's frustule—a thickened cell wall made of cellulose that provides protection. The way the theca is arranged around the dinoflagellate results in at least 6 different known configurations that aid in classification.



- Although they are not the only algal group to do so, certain species of dinoflagellates are notorious for their formation of harmful algal blooms under certain conditions. These are commonly known as red tides and are the result of the dinoflagellates breeding at such high concentrations that they turn the water red, almost the color of blood. In reality, it's just a reflection of the color of the photosynthetic pigments within the individual cells.

- Although it is unclear why they might do so, certain species manufacture extremely harmful toxins. The concentration of these toxins per individual dinoflagellate cell is negligible, but under the right conditions—for example, if nutrients and light are bountiful—the subsequent bloom can raise toxin levels per unit volume to dangerously high levels.

- Filter or suspension feeders, such as bivalves, which typically forage indiscriminately, are particularly susceptible to the accumulation of these toxins. Then, if humans eat those bivalves—for example, a mussel or a scallop—the results can be deadly.

- Certain types of diatom can also create a harmful algal bloom. These are called brown tides, for similar reasons as red tides are so called, although the types of toxin involved are different, as are the potential medical consequences.

- Certain types of dinoflagellate form a symbiotic relationship with cnidarians to form coral. These are called zooxanthellae. Confusingly, some dinoflagellates are classified as heterotrophs—that is, nonphotosynthetic—and some as mixotrophs—that is, they are both auto- and heterotrophic.

- The final major component of the phytoplankton are the cyanobacteria, what used to be referred to as the blue-green algae before we realized that they were prokaryotic in design. The cyanobacteria are an extremely ancient phylum within the domain Bacteria, dating back perhaps as far as 2 billion years

ago. Through their photosynthesis, they may well have been some of the first organisms to start oxygenating our atmosphere, an event that had an incalculably important effect on the future life on our planet, which is now for the most part aerobic.

> To some extent, the oxygen you breathe comes from the terrestrial plants around you, but at least 50% comes from phytoplankton, and within the phytoplankton, probably about half comes from diatoms alone.

- Also extremely important is cyanobacteria's ability to fix nitrogen, an ability known as diazotrophy. This means that they can take the raw, inert nitrogen gas of our atmosphere and convert it to metabolically useful compounds, such as nitrates, nitrites, and ammonia. Nitrogen is an essential element in amino acid, and therefore protein construction, as well as in nucleic acid formation. There is no other way for eukaryotic metabolism to get this nitrogen other than through the fixation process performed by diazotrophs.

LECTURE SUPPLEMENTS

Readings

Amaral-Zettler, Artigas, Baross, Bharathi, Boetius, Chandramohan, Herndl, Kogure, Neal, Pedrós-Alió, Ramette, Schouten, Stal, Thessen, de Leeuw, and Sogin, "A Global Census of Marine Microbes."

Castellani and Edwards, eds., *Marine Plankton*.

Castro and Huber, *Marine Biology*.

Mladenov, *Marine Biology*.

National Oceanic and Atmospheric Administration, "Harmful Algal Blooms."

Sardet, *Plankton*.

Townsend, *Oceanography and Marine Biology*.

United States Environmental Protection Agency, "Harmful Algal Blooms."

Web Resource

Smithsonian Institution, "Ocean Portal: Plants and Algae," http://ocean.si.edu/ocean-life-ecosystems/plants-algae.

Questions to Consider

1. What is the difference between an autotroph, a heterotroph, and a mixotroph? Provide examples of each.

2. Draw a marine food web cycle that orders the following components: bacterial decomposer, bluefin tuna, diatoms, sardines, and copepods.

3. Find your closest coastline (if you can't decide, choose Florida in the United States) and research what species of algae might produce harmful algal blooms in your area. What local weather or oceanographic events seems to predict the bloom's occurrence?

4. Some cyanobacteria play an incredibly important role in the ecosystem by converting inert nitrogen gas to metabolically useful species of nitrogen. Why is this so important?

5. You've probably seen campaign advertisements to save various endangered species, regardless of how important that species is in terms of ecosystem services. How would you design a similar campaign to save phytoplankton? What talking points would you use?

7

INVERTEBRATE LIFE IN THE OCEAN

This lecture is about the invertebrate phyla that are found in the ocean. A majority of these will be important components of the zooplankton, who drift on ocean currents during at least some of their life. You will encounter species that inhabit the benthic (which refers to the seafloor) environment; you will meet both infauna—species living inside the sediments of the seafloor—and epifauna, species living on the surface of the seafloor. Some benthic animals are mobile while others are sessile, meaning that they are fixed in one place. You will also discover animals capable of moving significant horizontal distances under their own locomotion; such animals are nekton, who can swim independently of currents.

Sponges

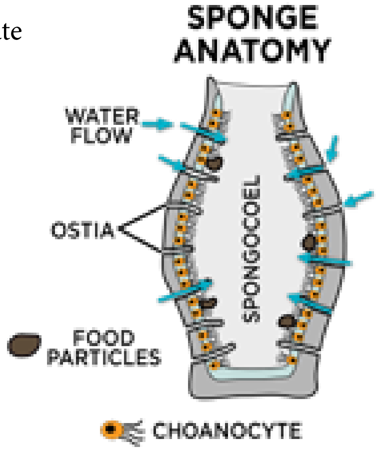
- Sponges belong to the phylum Porifera, within a small subkingdom called the Parazoa, which translates to mean "like animals." Classifying sponges presents a challenge because they do not possess tissue and organ structures like an animal does, nor do they have a nervous system with which to investigate the environment or a circulatory system with which to circulate products and reactants of metabolism.

- They are nonetheless a very prolific, sessile, benthic epifaunal organism, with more than 5000 species currently identified, found in almost all oceanic regimes, from the abyssal plain to the sublittoral and littoral zones.

- Sponges are suspension feeders, meaning that they feed on tiny particles of food suspended in the water column. They do this using specialized flagella-armed cells called choanocytes that waft water through channels called ostia into the interior of the organism. In this way, choanocytes catch particles of food—typically bacteria and phytoplankton—and draw them into the body of the organism.

- Sponges have primitive endoskeletons that are reinforced with either silicon or calcium carbonate, depending on the species. Sponges are for the most part heterotrophic, and a few sponges are apparently carnivorous.

◇ As is a theme in most invertebrate and some vertebrate animals, sponges use a planktonic phase to distribute gametes and disperse other cells, which then can become new sponges. This is part of the secret as to why sponges are so widely distributed in our oceans: They hitch a free ride on the oceanic currents.



◇ A parallel group to the Parazoans are the Eumetazoans, or true multicellular animals, where you will find all the other animals, including humans. Now that the body is more than one cell big, how do cells coordinate their activity? Multicellular organisms work around this problem by specializing certain cells into tissue types. Tissues go on to make organs, and organs make up organ systems. Key to all the animals we will review from now on will be this complexity and hierarchy of cellular organization.

Cnidarians

◇ The marine Eumetazoans include the Cnidarians, all of which possess a specialized form of cell known as a cnidocyte, or stinging cell. A cnidocyte has the ability to send out a long organelle that can either attach itself to prey or inject a hypotoxin.

DID YOU KNOW?

Tentacles can continue to sting long after they have become detached from the jellyfish!

- Cnidaria can be broadly divided into 3 groups: the polyp-producing Anthozoa, in which we find corals and sea anemones; the Medusozoa, which are the jellyfish; and the Myxozoa, which are principally parasitic.

- Cnidarians are radially symmetrical and have relatively simple body designs. Jellyfish are planktonic for a majority of their life cycle but have a brief sessile stage; Anthozoans, on the other hand, are principally sessile except for their planktonic dispersal phase.

- Feeding methods are similar across the phylum, whereby cnidocyte-armed tentacles catch and direct prey toward a mouth that opens into a gastrovascular cavity. Waste is pushed out through the same mouth opening.

- In spite of their name, comb jellies are not jellyfish but belong to a separate phylum known as Ctenophora. They have a similar morphology to jellyfish, but they lack stinging cells and have a unique method of locomotion: rows of cilia that are spaced so close together that they scatter light, emanating a rainbow of colors along the cilia as the organisms move. In addition, many ctenophores are bioluminescent.

Marine Worms

- ◇ Bilateria are organisms that are bilaterally symmetrical. This was an important evolutionary step because it gave an animal's body direction. A bilaterally symmetrical organism can have an anterior, posterior, left, and right. And because the front end of the organism is more likely to encounter new aspects of the environment first, we can start to pack sensory systems at that end, and perhaps some neural cells to help process that information. A concentration of neural cells can eventually lead to a brain, and this was the preadaptation that led to that important organ.

- ◇ The first bilaterians were various forms of worm: flat, round, and segmented.

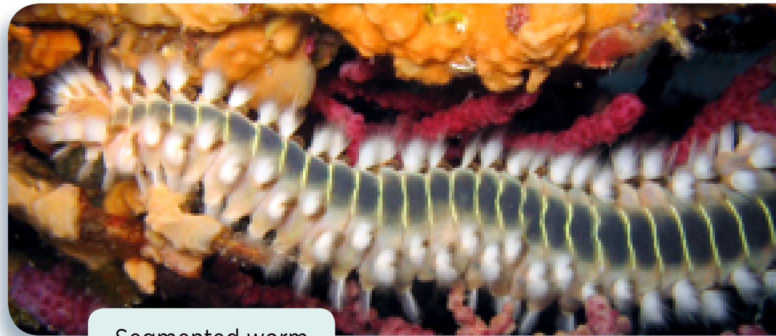
  1. Flatworms, from the phylum Platyhelminthes, are divided into several classes. Most are parasitic, but those that are free living are predatory in nature. Flatworms lack a circulatory system and instead rely on the natural process of diffusion to move metabolites around the body. There is only one opening into the gastrovascular cavity. In their larval dispersal forms, all flatworms are planktonic.

Flatworm

2 Roundworms, or nematodes, are an extremely diverse group that have exploited pretty much every niche available in our oceans. Some can be found as plankton while others are part of the infauna of the benthos. Roundworms are the first animals we have encountered thus far to have a rudimentary intestinal tract, with a separate mouth and anus. This is a feature that we will see in the rest of the animals we encounter.

Roundworm

3 Segmented worms, or annelids, are another successful group of organisms that occupy many niches within the ocean, typically benthic. Most of the marine representatives in this phylum belong to the class Polychaeta. All annelids consist of a series of segments, a useful development in the evolution of body design. Like the tubular gastrointestinal tract, segmentation is a theme that will be seen in the remainder of the animals that will be addressed in this lecture.



Segmented worm

Mollusks

- Species in the phylum Mollusca are highly diverse, ranging from the tiniest of nudibranchs, measuring a few millimeters in length, to the colossal squid, measuring more than 10 meters in length. Mollusks are in every environmental niche to be found in the ocean. Their larval forms make up a substantial portion of the plankton, and in their adult forms, they can survive the intertidal, sublittoral, abyssal plains, and deep-sea trenches.

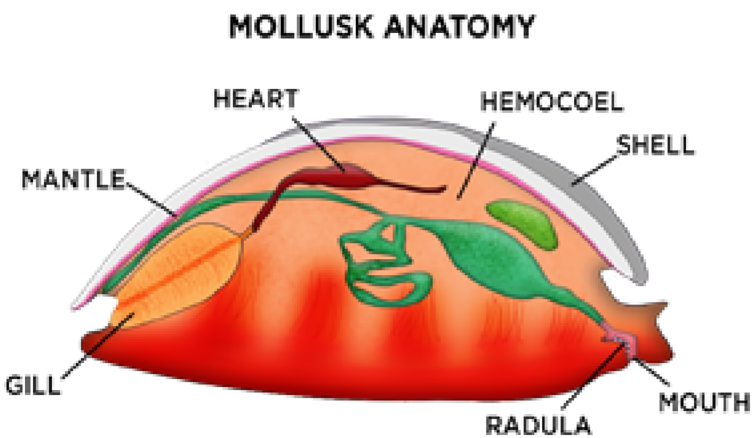
Nudibranch

- Major classes within the Mollusca include the Gastropoda, the Bivalvia, and the Cephalopoda. Among the gastropods are a number of single-shelled organisms, such as the limpets and abalone, as well as more naked species, such as the nudibranchs, sea hares, and sea butterflies. The Bivalvia include those organisms with 2 shell halves, such as clams, mussels, and scallops. The cephalopods include the octopus, squid, and nautilus.

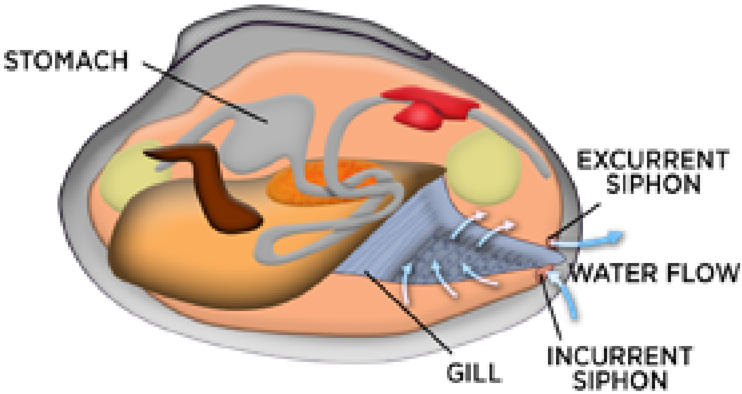
- Despite their highly diverse forms, all mollusks have a mantle. If the mollusk has a shell, then the mantle is responsible for its formation, which is done through a biomineralization process that takes carbon dioxide dissolved in the water column and converts it to carbonate.

- Mollusks, like most marine segmented worms, get their oxygen through gills. They also have a primitive circulatory system and a heart to pump fluid through that system, although we would term the system "open." This means that there are very few pipes or vessels leading circulatory fluid one direction or another. Instead, the animal has a large internal cavity, referred to as a hemocoel, that bathes the internal organs in that fluid. Because that fluid is mostly water and therefore incompressible, the hemocoel also acts as a hydrostatic skeleton, and by contracting muscles around various parts of the hemocoel, the mollusk can move around.

- Feeding in the mollusks is also highly diverse. Many mollusks have radulas, a roughened tonguelike structure rather like a metal file. In herbivorous species, the radula is used to scrape food from a surface. In some of the more predatorial species, the radula has been converted into a drill, allowing them to burrow into the shell of other mollusks. In the cone snails, the radula has been modified into a harpoon laced with a venom that can be deadly to humans.



BIVALVE ANATOMY



- Bivalves do not have a radula; instead, they filter-feed using a pair of siphons to bring water into the organism and back out. Within the organism, the water flows over the gills, oxygenating the circulatory fluid. However, in bivalves, the gills are not just responsible for gaseous exchange. They are also coated with a mucus that traps food particles; tiny cilia that line the gills then push food toward the stomach.

Be careful what you pick up on the beach! There is a cone snail that is commonly referred to as a cigarette snail, because once stung, you only have time for one cigarette before you die!

- The nervous system of a mollusk is quite well developed. The pinnacle of neural development in the mollusks is in the cephalopods: the squid and octopus.

- Squid, which are also cephalopods, can form schools that can be a valuable source of food for other animals, especially marine mammals. However, at least 2 species of squid are more solitary and can gain enormous size: the giant squid *Architeuthis* and the colossal squid *Mesonychoteuthis*.

- While mollusks do have mobility, for the most part it is confined to movement across the benthos, although the cephalopods are a clear example of nekton—free-swimming species that are independent of currents. That said, pretty much all mollusks enjoy some time in their larval stages as zooplankton.

Arthropods

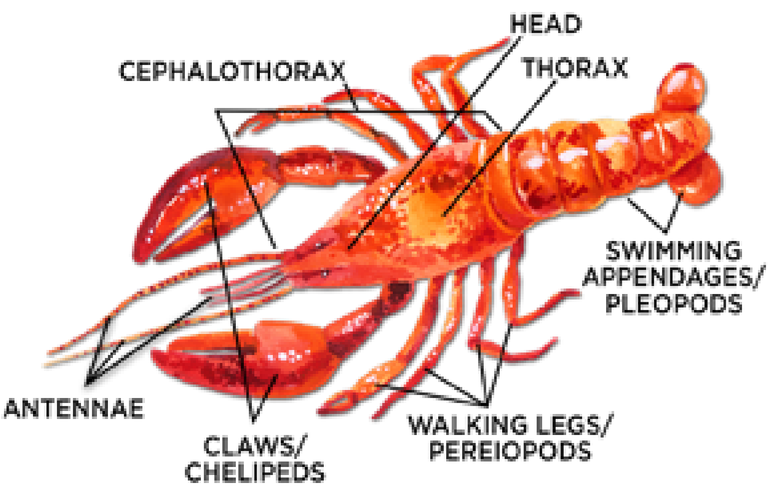
- The next phylum is Arthropoda, which means "jointed foot." Within the arthropod body are regions that we refer to as the head, thorax, and abdomen. Each of these regions is made up of segments, each with the potential for a pair of appendages that can be highly specialized.

- All arthropods have a jointed, hard exoskeleton reinforced with chitin. Their limbs are articulated and thus capable of very fine, delicate motor movement. However, their hardened exterior limits growth, so arthropods must molt their exoskeleton from time to time; a new, temporarily softened exoskeleton awaits beneath and expands with the quick growth of the arthropod following the molt, and then hardens.

- Marine arthropods range in size from microscopic, and therefore typically planktonic, to the 4-meter leg span of the Japanese spider crab. Marine arthropods come from 2 clades. The first of these, the Chelicerata have a pair of modified mouth parts known as chelicerae that are used to hold food. This group would include the sea spiders and horseshoe crabs, both of which have a benthic lifestyle, foraging on various invertebrates. Their larva are planktonic.

- The second marine arthropod clade are the crustaceans, a large taxonomic group that contains almost 70,000 species. This subphylum contains a large range of classes, 2 of which are the Maxillopoda, which includes the copepods and the barnacles, and the Malacostraca, which includes the crabs, lobsters, krill, shrimp, and amphipods. Both of these classes are planktonic in their larval form; some, such as krill and certain copepods, are planktonic throughout their entire life history.

ARTHROPOD ANATOMY



Echinoderms

- The last exclusively invertebrate phylum is Echinodermata, which translates to "spiny skin." This group contains the sea stars, brittle stars, sand dollars, sea urchins, and sea cucumbers, as well as sea lilies. They are an exclusively benthic marine phylum and can be found anywhere from the intertidal down to the abyssal plain.

- In the echinoderms we see a return to radial symmetry in the adult form—a specific kind of radial symmetry known as pentaradial symmetry, one based on units of 5. However, all echinoderms have a planktonic dispersal phase, and those larvae are bilaterally symmetrical, justifying their classification in the Bilateria.

- Perhaps one of the most interesting innovations in the echinoderm is its internal hydraulics—known as the water vascular system—that makes use of a network of canals filled with water. Using muscles to constrict parts of those canals forces water down toward the distal end of the canals, known as tube feet. In this way, the hydraulic system can be used to move the organism, and help it cling to prey.

LECTURE SUPPLEMENTS

Readings

Bucklin, Nishida, Schnack-Schiel, Wiebe, Lindsay, Machida, and Copley, "A Census of Zooplankton of the Global Ocean."

Castellani and Edwards, eds., *Marine Plankton*.

Castro and Huber, *Marine Biology*.

Johnson and Allen, *Zooplankton of the Atlantic and Gulf Coasts*.

Maine Department of Marine Resources, "Maine Lobster."

Martinez, *Marine Life of the North Atlantic*.

Miller and Wheeler, *Biological Oceanography*.

Mladenov, *Marine Biology*.

National Geographic Society, "Krill."

Rosenfeld, *The Intertidal Wilderness*.

Sardet, *Plankton*.

Thompson, "Krill Are Disappearing from Antarctic Waters."

Web Resources

Smithsonian Institution, "Ocean Portal: Invertebrates," http://ocean.si.edu/ocean-life-ecosystems/invertebrates.

———, "Ocean Portal: Plankton," http://ocean.si.edu/ocean-life-ecosystems/plankton.

Questions to Consider

1. The lecture mentions a resemblance between Poriferan choanocytes and protistan choanoflagellates. What are the similarities between these 2 cells, and why is the choanoflagellate believed to be an important missing link in determining the origins of kingdom Animalia?

2. The animals reviewed in this lecture can also be divided on the basis of being diploblastic or triploblastic. Within the triploblasts, one can be acoelomate, pseudocoelomate or eucoelomate. What do these terms mean? Using these terms, how would you classify a roundworm? An octopus? A jellyfish?

3. Review how cnidocytes work and the variation in their design.

4. Track the life cycle of the American lobster, *Homarus gammarus*, from egg to adult form through its various molts. At what point does it start to actually look like a lobster?

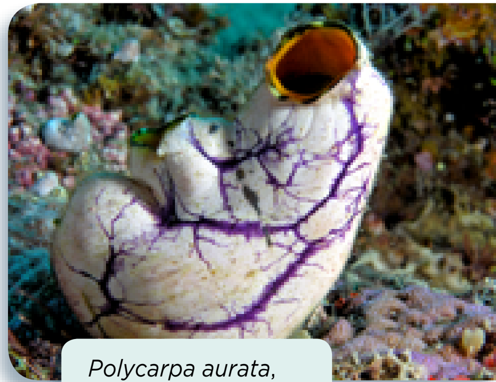
8

AN OVERVIEW OF MARINE VERTEBRATES

The food web diagram reveals how deeply all ocean life ultimately depends on the very small planktonic forms at the base of the web, including all those species of invertebrates that have a planktonic life stage. But more commonly, when we think about life in the ocean, we tend instead to think about the vertebrate species, because those are the ones that have more commercial and cultural importance to us. This lecture will continue the journey up the food web and prepare for a more in-depth look at marine vertebrates.

Chordates

◇ The previous lecture examined animal phyla that were exclusively invertebrate in nature—that is, lacking a backbone. The final phylum, Chordata, includes 2 invertebrate subphyla—Tunicata and Cephalochordata—and the clade Craniata, which includes all vertebrates.

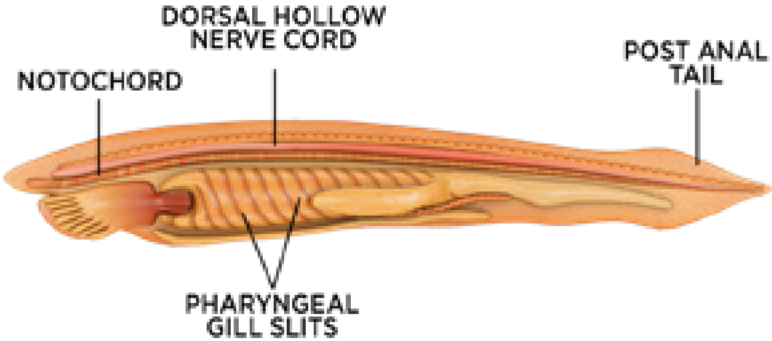


Polycarpa aurata, a variety of tunicate

◇ All chordates have, in some of part of their life history, 4 features in common: a stiff rod known as a notochord that runs the length of the animal, a dorsal hollow nerve cord, a postanal tail, and pharyngeal gill slits.

◇ Tunicata includes the tunicates and salps, both of which are exclusively marine. Tunicates look like sponges and, similar to sponges, are filter feeders; however, their body design is much more complex. Salps are jellylike filter feeders that are planktonic their entire life, foraging on phytoplankton. Salps can reproduce at extremely fast rates for such a complex animal and can have an important grazing impact on phytoplankton.

◇ Cephalochordates are also exclusively marine; this group contains the lancelets, which are often considered as the stereotypical chordate because they have all of the qualities of a chordate represented in their adult form. Like tunicates, they are also filter feeders, living buried in the sediment.



- The last clade in the last phylum is Craniata. Species within this group are so named because of the existence of a cranium, a series of bones fused together to protect the brain. In other words, they possess skulls.

- Craniata includes 3 subphyla: the hagfish, the lamprey, and the vertebrates, although researchers are still trying to decide whether the lamprey might be better included inside the vertebrate group. For now, we will place them in their own subphylum because of their unique characteristics that allow them to serve as a link between the more primitive chordates, such as the hagfish and the true vertebrates.

- Hagfish are exclusively marine, while lamprey have both marine and freshwater species. Both are characterized as having eellike bodies, and both are scavengers. Some are even parasitic. Neither group has jaws, but both have sharp teeth that allow the animal to cut and bore into the flesh of another animal—sometimes dead, sometimes alive.

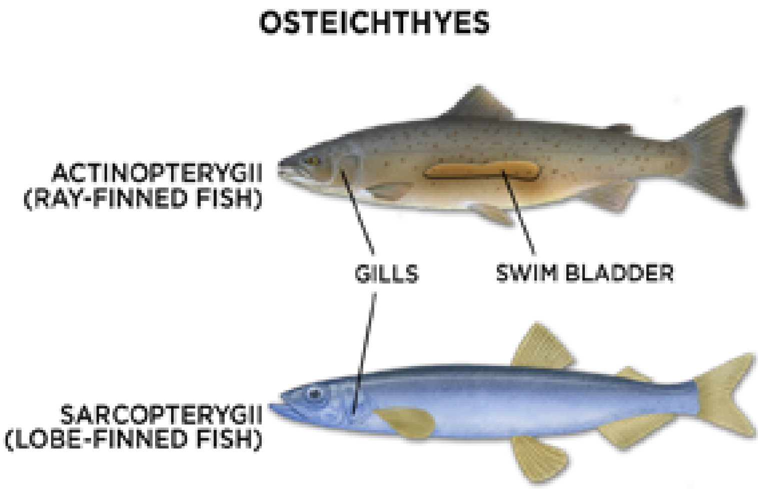
◇ Vertebrates form the third subphylum of Craniata. It is by far the most diverse group within Chordata, containing everything from dinosaurs to humans. However, only certain classes within Vertebrata have marine representation, including Chondrichthyes, the cartilaginous fish; Osteichthyes, the bony fishes; Reptilia, the reptiles; Aves, the birds; and Mammalia, the mammals. Vertebrates possess a true vertebral column, an evolution of the notochord, as well as true bony jaws in all the extant classes.

◇ Researchers are currently debating the correct classification of birds. We are now fairly certain that the clade Aves belongs within the Reptilia; after all, birds are living descendants of dinosaurs. For simplicity, we will treat them as a separate class.

◇ Chondrichthyes contain the sharks and rays. This class can be divided into 2 subclasses: the Holocephali, which include the ratfish, and the Elasmobranchii, which include the skates, rays, and sharks. Almost all of the species in Chondrichthyes are marine, although there are a few examples of freshwater sharks and rays. All chondrichthyans use cartilage, rather than bone, to build their skeleton. This makes their skeletons more flexible.

◇ The fish within superclass Osteichthyes have calcified bones for their skeletons. It's a highly diverse class, including the Actinopterygii, or ray-finned fishes, and the Sarcopterygii, the lobe-finned fishes, the latter believed to be the ancestors of amphibians.

◇ Osteichthyans are not exclusively marine. However, all bony fish possess a swim bladder, which helps the fish maintain neutral buoyancy. Cartilaginous fish do not possess a swim bladder and must rely on other adaptations to stay neutrally buoyant in the water column.

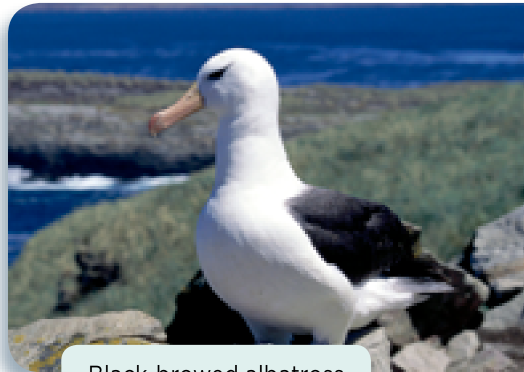


- Both bony and cartilaginous fish use gills to extract dissolved oxygen from the water, although some lobe-finned fish, specifically the lungfishes, have primitive lungs that allow them to breathe air.

- There are several species within the Reptilia class that hunt or spend sufficient amount of time in the marine environment to be considered marine. Because this class represents animals that first evolved on land and then returned to the ocean, all the species within it have lungs. Therefore, all marine reptiles are the equivalent of snorkelers and must endure periods of apnea while submerged.

- A number of bird species have developed a dependence on the marine environment, but all must return to land to nest. That said, some birds are remarkably well adapted to a marine lifestyle—for example, the penguins are as accomplished and diverse as some marine mammals. Other birds have evolved

to hunt in the shallow waters of the marine environment, including various species of surface-diving and plunge-diving birds. Other than to nest, some species spend almost their entire life at sea—for example, the albatross. In many marine food webs, birds often are an apex predator.



Black-browed albatross

- Within the mammals, there are 5 groups that have returned to the marine environment, including the sea otters, sirenians, pinnipeds, cetaceans, and polar bears. As animals that evolved from terrestrial, lung-possessing ancestors, all marine mammals must hold their breath when they dive. Nonetheless, marine mammals are some of the most capable divers in the animal world.

- Finally, *Homo sapiens* is a species that plays an important, influential role in the ocean. Humans are extremely efficient marine predators—so much so that we have the power to completely exterminate certain species targeted through fisheries. Human-caused mortality for some species is extremely significant, whether it's because we intend to eat them or because the take is incidental to our processes for living.

- Humans are one of a series of apex predators at the end of the complex food web. Our most direct immediate influence is on the nekton—for those are the species that are desirable as food—the large fish, for some countries the whale, and so on. However, we also have an indirect influence on the lower, planktonic trophic levels by impacting the environment in which they live.

The Interplay between Species

- In the food web, primary producers are eaten by herbivorous primary consumers, which in turn are fed on by a series of secondary and tertiary consumers, up to an apex predator. At each of these trophic levels, there is an opportunity for organisms that die naturally to be returned back into the cycle through decomposition. However, this trophic process is inefficient; not all the biomass created at one trophic level passes on to the next.

- In the ocean, pretty much all food webs start with phytoplankton, unless you exist in the aphotic zone, where there is no light. In the presence of nutrients and light, as well as the reactants carbon dioxide and water, these algae photosynthesize to produce complex sugar molecules. These molecules are metabolically processed to help the cell grow.

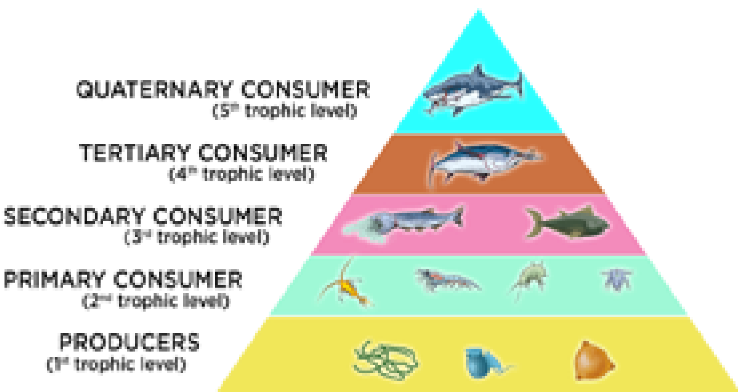
- Once the cell grows sufficiently, it might reproduce, making more algae. One algal cell becomes 2, which becomes 4, which becomes 8, and so on, creating the algal bloom that is such a necessary part of the beginning of the trophic process.

- Along comes the primary consumer, or herbivore: the copepod. Physically, that herbivore—even if it numbers in the millions—cannot consume all the algae. Some will escape. Also, once in the gastrointestinal tract of the copepod, not all of that algae will be consumed; some will be voided from the gut unprocessed as fecal pellets.

- Not all of the phytoplankton that is processed will even go toward growth. Some will be used immediately by the copepod to release energy, used to power the organism's metabolism. Eventually, once all the processes are considered, only a small portion of what was originally available at the previous trophic level can be used to help the population of copepods grow.

- ◇ This inefficiency happens at each trophic level. The biomass available at one trophic level will always be some fraction of that which was available on the previous level. Scientists believe that with a whole bunch of error bars, caveats, and assumptions, the fraction can be estimated at about 10% per trophic level. In other words, the biomass created at one trophic level is 10% of that at the next level down. In reality, sometimes that value is higher, and sometimes it's lower.

- ◇ Another way to visualize this is as a pyramid. The base of the pyramid represents the sum total of primary production; the next tier represents the sum total of primary consumers, or herbivores; the third tier represents the secondary consumers, or carnivores; and so on. Because the process of trophic transfer is inefficient, each subsequent tier is smaller than the next, creating the pyramid shape. At the very top of the pyramid—at its apex—are the apex predators.



APPLYING THE 10% RULE

An adult male humpback whale typically weighs 35,000 kilograms. To make a 35,000-kilogram humpback whale, you would need 10 times that amount in capelin, so that's 350,000 kilograms of capelin over the lifetime of that whale. To make 350,000 kilograms of capelin, you would need 3,500,000 kilograms of copepods, who in turn need 35,000,000 kilograms of phytoplankton, or 35,000 metric tons.

In other words, that humpback whale represents 35,000 metric tons of reprocessed algae over its lifetime!

- Some ocean managers have thought that perhaps they can calculate the ocean's potential to provide fish for the human population by measuring the global phytoplanktonic productivity and then using the 10% per trophic level rule to see how many fish that makes. Such a calculation, if it were viable and practical, could provide an important insight into whether the oceans can support the planet's burgeoning human population.

- Of course, the oceans do not have limitless potential. In fact, their potential is quite finite, although arriving at an actual number might be impractical because of the statistical errors involved.

- Such calculations also make a basic assumption about the stability of the ocean that is often not appropriate. Oceanic primary productivity from year to year is highly variable because primary productivity occurs at the whim of oceanographic processes that are variable from year to year. Maybe in one year, a particular water mass dominates over another and has less nutrient load. Maybe in another year, the water is slightly colder and can therefore hold more dissolved oxygen and carbon dioxide. All these things can dramatically affect productivity.

- We characterize these large-scale influences as bottom-up effects, in the sense that the ecosystem is impacted by changes that are happening at an oceanographic level, influencing the bottom of the marine ecosystem web. There are also top-down effects, whereby a predator can have such an overwhelming negative impact on a prey species that it has a knock-on effect on other competing predators, as well as that prey's prey—which would experience at least a temporary release from predation.

- These types of phenomena can be completely natural, and potentially completely unpredictable, although researchers, especially those interested in characterizing the behavior of populations over time, do try very hard to model them—with some success.

- While the static representation of the food web is complicated enough, in reality the image needs to be animated, with natural bottom-up and top-down effects influencing the size of the individual populations of each species, and therefore the volume of flow between species in terms of biomass trophic transfer. Because these effects are largely unpredictable, their impact is chaotic—but they would occur as pulses that would have a knock-on effect as you move up through each trophic level.

◇ Then add to that humans' capacity as a predator to have dramatic top-down effects on key species that are commercially important, such as herring, cod, mackerel, and tuna. Beyond that, add the much more insidious and even less predictable bottom-up effects we might be causing in the system due to global climate change and ocean acidification.

LECTURE SUPPLEMENTS

Readings

Block, Costa, and Bograd, "A View of the Ocean from Pacific Predators."

Liem, Bemis, Walker, and Grande, *Functional Anatomy of the Vertebrates*.

Philander, *Our Affair with El Niño*.

Questions to Consider

1. Review the differences between hagfish, lampreys, chondrichthyans, and osteichthyans (differentiating between Actinopterygii and Sarcopterygii) in terms of skeletal structure (including jaw and fin structure).

2. Review the impacts of El Niño and La Niña on southeastern Pacific productivity. How does the oceanography of these 2 conditions affect the Peruvian anchovy population? Does this have knock-on effects on other species?

3. The impact of sea otters on local sea urchin populations has been described as substantial and an example of a top-down-regulated system. Speculate on how a decrease in transient killer whale populations (a known predator of sea otters) might impact levels of kelp (a known food source for sea urchins).

9

FISH: THE FIRST VERTEBRATES

This lecture focuses on fish, the first group of vertebrates in our ever-expanding phylogenetic tree of marine life. Fish, the first vertebrate chordates to evolve, are an extraordinarily diverse taxonomic group. They vary in shape, form, and color; they vary in lifestyle, habitat, and behavior. They differ vastly in physiology and capacity. Yet fish are unified in many ways by the solutions they have adopted, through the pressures of natural selection, in answer to the challenges of the ocean environment.

Chordates

- Fish are a remarkably successful and diverse group, and can be found in most regions of the ocean. Although some are herbivorous or planktivorous, a number have become very successful predators, occupying the apex positions in the food chain.

- Most fish are ectothermic, or cold-blooded, but a few have developed forms of endothermy; in other words, they have the equivalent of their own central heating system, powered by the energy of cellular metabolism.

- Some fish are ecologically essential, performing vital ecosystem services and forming important trophic links between planktonic invertebrates and higher-level predators. Many have a planktonic larval phase and therefore as young form an important part of the prey community for lower-trophic-level carnivores. Many species are important to humans, and some species have been fished to the point of commercial extinction.

- Fish are craniate members of the phylum Chordata. All chordates have 4 essential characteristics: a spine-stiffening rod known as the notochord, a dorsal hollow nerve cord, pharyngeal slits, and a postanal tail. In addition, as craniates, fish possess a cranium, or skull, that protects the brain. Each of these characteristics has been derived somewhat in the fish—meaning that these traits have significantly evolved away from a prototype.

- Fish can be broadly divided into so-called jawless and jawed kinds. Jawless fish, or the agnathans, include the hagfish and lampreys. Agnathans are referred to as jawless because rather than the strong, leverage-providing jaws of later fish species, they simply have rows of teeth.

Sea lamprey (*Petromyzon marinus*)

- The jawed fish have developed bony levers, called jaws, on which to situate the teeth. From this point on, all vertebrates have jaws. From an evolutionary point of view, the development of jaws was an important step forward, allowing fish to become much more efficient predators and allowing them to firmly grasp their food.

- Jawed fish appear in the fossil record around 425 million years ago, in a now-extinct group of fishes called the placoderms. A second group of early, now-extinct fish known as the spiny sharks, or Acanthodii, also appeared to have jaws; this group, along with one other, the Ostracoderms, eventually gave rise to the chondrichthians, a group still extant today, into which we place sharks, skates, and rays.

- As chordates, chondrichthians do possess a notochord during their larval phase; however, this is soon replaced by a cartilaginous vertebral column. In fact, chondrichthians are mainly distinguished by the use of cartilage, rather than bone, for their internal skeletons. Cartilage is a tissue similar to bone, but less rigid and more flexible. However, it retains sufficient rigidity for it to serve a skeletal function. Because of this predictable association, we often refer to sharks, skates, and rays as the cartilaginous fish.

- This is in contrast to the final group in this taxonomic clade, the bony fish, or osteichthians. In the bony fish, the cartilaginous material that makes up the internal skeleton has been replaced by bone. We divide this group into 2 broad groups: the Actinopterygii, the ray-finned fish, and the Sarcopterygii, or lobe-finned fish. As the names suggest, we differentiate these 2 groups by the structures underlying their fins.

- The fins of a ray-finned fish are supported by a series of spines that radiate out, between which the webbing of the fin is suspended. In contrast, the fins of a lobe-finned fish are fleshy. In terms of evolution, this was an important innovation, as it was from the lobe-finned fish that the terrestrial tetrapods evolved.

Pygocentrus nattereri,
a variety of ray-finned fish

Adaptations

- It's important to remember that fish evolved in the ocean, so we can expect to see that they are highly adapted to an aquatic environment. This is in contrast to some of the taxonomic groups we will encounter later that evolved on land and then returned to water, and thus have had to secondarily readapt to a watery environment.

- A watery environment places very specific selection pressures on a developing organism. Water is much heavier and more viscous than air, and therefore natural selection will favor a streamlined

organism. Water is also a 3-dimensional environment, so organisms—through the process of evolution—must address the issues of buoyancy and the challenges of living at pressure-crushing depths.

- And while oxygen is available in water, it is present in much lower partial pressures than it is in air, so aquatic animals must, through evolution and natural selection, figure out a way to extract dissolved oxygen from the water column. Moreover, water is relatively opaque to light, so organisms must rely on senses other than vision to interrogate the environment.

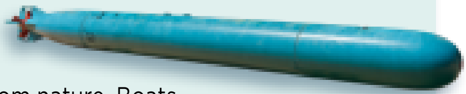
Body Shape

- All bodies moving through a fluid experience the phenomenon of drag. The more viscous the fluid, and the less streamlined the object, the higher the drag, and therefore the more energy an organism has to expend to counter that drag. To reduce the amount of energy used in swimming, natural selection will favor body designs that minimize drag in highly viscous environments such as the ocean.

- An important predictor of drag is the relative speed of the object moving through the medium. Faster objects experience more drag. Thus, really fast-moving fish are more streamlined.

- Drag also depends on the surface area of the body that is in contact with the fluid as a frictional surface. Thus, compared to humans, fish have relatively simple bodies with few folds and no more appendages than necessary.

WHY ARE TORPEDOES SHAPED LIKE TORPEDOES?



The simple, fusiform shape of the torpedo is the shape that is the most streamlined. In this case, humans took a lesson from nature. Boats, submarines, and so on are all versions of the fusiform shape that fish evolved.

- Finally, drag depends on the shape of the swimmer, an aspect that can be characterized in a constant known as the drag coefficient. All fish, in general, tend to have very similar, sleek, torpedolike shapes. There are definitely variations across the various fish taxa: Some are snakelike, such as the lampreys, hagfish, and eels; some have been dorsoventrally compressed, such as the rays and bony flatfish; some have been laterally compressed, such as the angelfish; and some—the ones that appear large, ungainly, and very unstreamlined—are simply species that do not need to consider the problem of drag as a particular challenge.

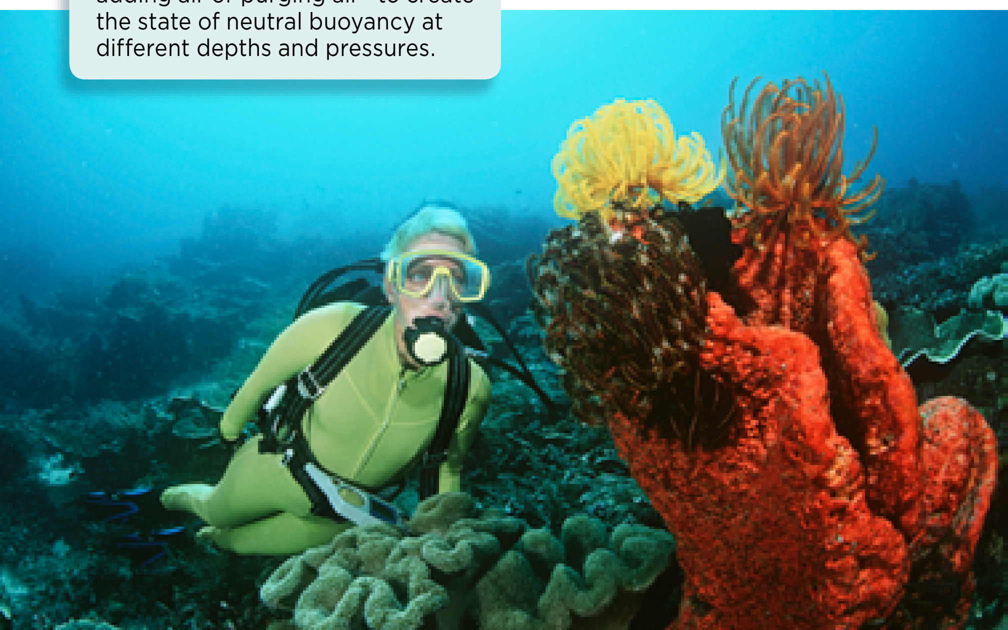
- There is also a huge variation in fish caudal fin shape. The caudal fin is the tail fin, and its shape depends on the lifestyle of the fish. The caudal fin is usually the main propulsive paddle in a fish, although there are exceptions. Fish that rely on quick maneuverability versus long-distance swimming have different-shaped tails: A lunated tail, which looks like a quarter-moon, is the tail of a long-distance migrator and predator capable of great sustained speed, while a rounded tail is much better for maneuverability and quick sprints.

Buoyancy

- Most bony fish possess a swim bladder. As a fish dives to greater depths, the weight of the water above the fish—experienced as pressure—will cause the swim bladder to compress. Because of the laws of buoyancy, the organ would not provide the same amount of lift at depth because it is displacing less water.

- To get around this problem, the organ can be inflated further using a gas gland. As the fish surfaces, the swim bladder expands because of less ambient pressure, and gas can be removed from the bladder by diffusion. This allows the fish to maintain neutral buoyancy at any depth. In this way, the fish minimizes the amount of energy expended in maintaining buoyancy.

Human scuba divers mimic the ability of fish to maintain neutral buoyancy by means of a buoyancy compensator that the diver is constantly adjusting—either by adding air or purging air—to create the state of neutral buoyancy at different depths and pressures.

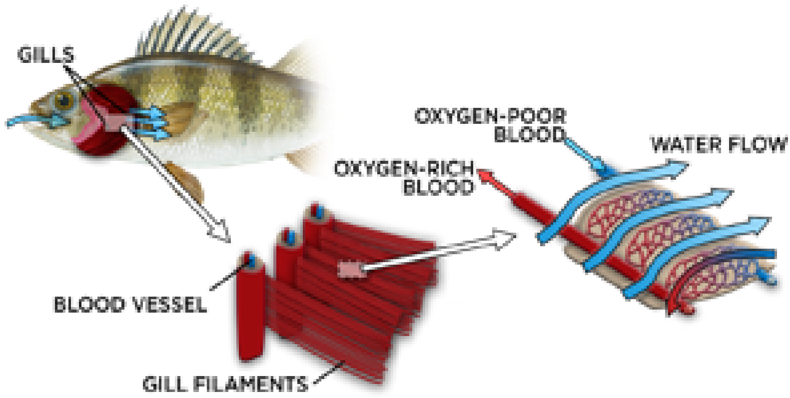


- Sharks, which should be considered the more ancestral form of fish, do not have swim bladders and create buoyancy using 2 strategies: Sharks have comparatively enormous livers, filled with an oil that is less dense than water, creating buoyant uplift; and a shark's pectoral fins are angled in such a way as to create lift as the shark swims forward. However, some shark species—and some bony fish, too—have simply chosen to be negatively buoyant, living on the seafloor.

Breathing

- All fish are aerobic—like humans, they need oxygen to burn their food to release energy. While there are a few lobe-finned fishes, such as the lungfish, that can extract oxygen directly from the air, for the most part fish must extract oxygen that is dissolved in the water column. This is done through the passive process of diffusion across a very thin membranous surface known as a gill.

- Gills are a finely structured series of capillary-sized vessels that come in direct contact with the water. Typically, water enters in through the mouth of the fish and moves onto the gills either through the forward movement of the fish or by a positive pumping action caused by the dropping of the jaw, causing water to rush in. Water then passes over the gills and out of the fish through an operculum, in the case of the bony fish, or gill slits, in the case of the sharks.



- Initially, as the water begins to pass over a gill, it contains a relatively high concentration of oxygen and low amounts of carbon dioxide. However, the blood in a vessel at the beginning of a gill contains a high amount of carbon dioxide and very little oxygen. These conditions set up diffusion gradients across which the gases will transfer. The water will offload oxygen and pick up carbon dioxide; the blood vessel will offload carbon dioxide and take up oxygen—which it can then deliver systemically to the rest of the body of the fish.

- The gill is designed so that the flow of blood across the gill is in the opposite direction to the flow of water across the gill. This sets up what is known as a countercurrent exchange that maximizes the efficiency of the gaseous exchange.

- In every instance known in nature of a diffusive surface such as this, natural selection has always chosen a countercurrent, rather than a concurrent, exchange system.

Sensory Ecology

◇ Fish live at all depths of the ocean and experience a variety of light conditions. At the surface, in the photic zone, light is not limited. Therefore, to an extent, in this zone, fish can depend on vision to sense their environment, although in highly turbid conditions, vision is limited. At depth, in the aphotic zone, there is no light. In this situation, natural selection has come up with the solution of bioluminescence: In short, if there is no light, make your own!

◇ This is done by raising a special molecule know as luciferin to its excited, light-emitting state, using a specific enzyme known as luciferase. This is typically done within bacterial cells that the fish will culture in colonies on the skin surface. In spite of this fascinating innovation, vision is still somewhat limited in water because of turbidity.

◇ Most fish do have reasonable vision, but it's only really useful across short distances. Many fish have developed excellent chemosensory abilities, particularly the sense of taste. Objects that leach tasteable chemicals into the water can often be located by following a concentration gradient in that particular sensory cue. The ability to find that object—for example, a bleeding fish—can be enhanced by adopting a zigzag search path that allows the predator to move in and out of that concentration gradient, determining its orientation.

◇ Some fish have developed relatively good hearing. Because sound is essentially a vibration, and chemically a fish is mostly water, a fish will tend to vibrate at the same rate as the water surrounding it. Therefore, to hear a sound, fish require a relatively dense hearing organ that does not vibrate at the same rate. Thus, at the heart of the fish ear is a heavy, dense calcareous stone known as an otolith.

- A few fish—herring for, example—have developed exceptional hearing, sensitive in the high frequencies. They do this by using their swim bladder as a sympathetic resonator.

- Finally, some fish have developed extremely unusual sensory systems that are only possible in water. For example, sharks are capable of detecting electric fields—an ability known as electrolocation. This ability helps sharks sense thrashing prey and may also enable them to detect and navigate by the Earth's magnetic field. Also, the highly pressure-sensitive lateral line organ allows a shark to detect tiny vibrations in the water, even the very fin beats of its potential prey.

LECTURE SUPPLEMENTS

Readings

Bone and Moore, *Biology of Fishes*.

Fuller, *The Great Auk*.

Liem, Bemis, Walker, and Grande, *Functional Anatomy of the Vertebrates*.

Moyle and Cech Jr., *Fishes*.

Philander, *Our Affair with El Niño*.

Web Resources

Smithsonian Institution, "Ocean Portal: Fish," http://ocean.si.edu/ocean-life-ecosystems/fish.

————, "The Division of Fishes," http://vertebrates.si.edu/fishes/.

Questions to Consider

1. What is a whale fall, and why is it ecologically important?
2. Consider a human Olympic swimmer. What adaptation does that swimmer undergo (both physically and behaviorally) to minimize drag?
3. Review why countercurrent exchange is so effective (compare with concurrent exchange). Find an example in the human world (either within our bodies or engineered by us) of a countercurrent exchange system.
4. Why hasn't electrosensitivity evolved on land?

10

MARINE MEGAVERTEBRATES AND THEIR FISHERIES

This lecture will take a holistic view of humans' relationship with the ocean in terms of biological resource extraction, and in the process, you will be introduced to the concept of the marine megavertebrates. Our relationship with these animals is complex. They often occupy the highest positions of the food web, as apex predators. They often taste good, and we have overexploited many of the species in this group and endangered their existence.

Marine Megavertebrates

- Marine megavertebrates, sometimes called marine megafauna, are the larger organisms that occupy the higher levels of the marine food web. All of the organisms in this category are vertebrates, thus falling into the phylum Chordata.

- There is no hard line defining how big a vertebrate needs to be in order to be considered "mega." In general, we reserve the term for the larger fish, such as the cartilaginous sharks and rays, and various larger bony fish perhaps a meter or larger, such as swordfish and tuna. The category also includes seabirds, sea turtles, and marine mammals, such as dolphins, seals, and whales.

- In almost all cases, our relationship with these megavertebrates started out with our exploitation of them as a source of food. Through time, as humans have become more aware of our almost-infinite ability to reduce animal species to extinction, we have placed a value on their preservation. And in some cases, we have evolved an entirely different relationship with these organisms.

The Mechanics of Fishing

- Most industrial-scale fishing is done from a boat that varies in size depending on how far out it needs to go into the ocean and the type of gear it needs to deploy. In these cases, it is useful to distinguish between the inshore and offshore fleets. Inshore boats, typically ranging 40 meters or less in length, ply the neritic waters that lie above the continental shelves—relatively shallow water within about 350 kilometers from land. In general, the smaller the boat, the less its capacity to move farther offshore.

By and large, we refer to the extraction of biological resources from the ocean as fishing and the industry that performs that act as a fishery—even though the species we are fishing may not be a fish!

For example, you hear talk of the lobster fishery or the seal fishery, neither of which is technically a fish. They nonetheless remain "fisheries" because the act of how one fishes is basically the same: One gets in a boat, travels out to sea, and then uses a cage, net, hook, or projectile to catch the target species.

- There is a concentration of biological activity in neritic waters, so it's not surprising that the inshore fleet is by far the larger and more active of the 2 fleets when considering fisheries globally. It is a convenient coincidence that most of the world's exploitable marine-based biological resources are relatively close to shore and thus can be accessed in relative safety.

- Inshore fleets use a variety of fishing methods that can generally be divided into active and passive fishing. Active fishing involves gear that is powered through the water using a boat. Passive fishing gear is set in the water column, either free-floating or anchored in some way to the seafloor and then later retrieved.

- Perhaps the simplest way to catch a fish is with a rod and line. However, this is not an efficient method at industrial scales, so instead a boat might choose to deploy long lines of rope with hundreds of baited hooks hanging from them—which is referred to as a longline fishery.

- In some cases, the line remains attached to the boat. In other cases, the line is floated at both ends with a flagged buoy that might even house a radio or satellite beacon to aid recovery. The line is then allowed to drift through the ocean, collecting its prize.

- Perhaps the most evolved "hook" in the business is the harpoon. Because it is so labor intensive, stabbing individual small fish is rarely profitable unless one is selling one's product to high-end local markets. However, individual megavertebrates can be so valuable in the market that sometimes harpooning is indeed a viable and extremely profitable business. Both swordfish and tuna, for example, are sometimes harpooned.

- Fishing nets can be either actively or passively used, and their size is limited only by the capacity of the boat from which they are fished. Active nets are more commonly referred to as trawls, and they can be massive indeed: A pair trawl is a net so huge that it needs 2 boats to tow it, with an opening the size of a football field.

The Tsukiji fish market in Tokyo has recorded some astronomical prices for individual fish. In 2013, a single tuna—weighing in at 222 kilograms—was sold for $1.8 million. That a single fish can fetch a price this high is a testament to how much we, as a society, enjoy eating tuna and how much we are prepared to pay for it.

- Passive nets are set, or anchored, in the water column and can be as simple as a panel of mesh. More complex nets create pounds into which fish can be herded; these can either be fixed in shape, as seen in cod traps, or they can be constricted on site in a process known as seining.

- Which fishing technique is chosen is a function of the behavior and size of the species targeted to be caught as well as where it is located both horizontally and vertically in the water column. For example, swordfish and sharks are typically fished using longlines, and shrimp and various flatfish are often trawled.

- Fishing offshore is physically wearing; boats, fishing gear, and crew have to be somewhat hardier. As a rule, pelagic waters are not as productive per unit area as neritic waters, so vessels may have to stay out longer to catch the same biomass as a fleet working inshore. Because such boats are fishing in deeper water, anchoring the gear is not possible; instead, the gear is typically either towed or set so that it will drift through the water for later pickup.

- Even with the added financial and physical investment in offshore fishing, the incentive is high, because even though many megavertebrates migrate huge distances across the open ocean, the potential profit if one can catch one justifies the expense.

- Fishing techniques vary in their selectivity. In rare cases, the fishing practice catches only what one wants it to catch. But almost inevitably, other nontargeted species are also caught. This is referred to as incidental bycatch. Sometimes, bycatch can also be sold at market for additional gain. However, it can also be the case that the bycatch represents species that we are not allowed to catch—often because the species is endangered or because fishing the species is unsustainable.

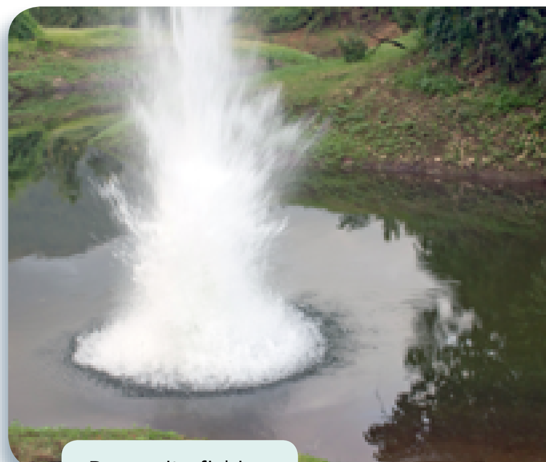
- Fisheries vary in the amount of bycatch they produce, and some are notorious for their bycatch levels. For example, shrimp trawling often yields more bycatch by weight than the actual shrimp themselves. At the most extreme, bycatch can be very problematic, especially if it involves a charismatic or endangered species.

- When a fishing practices creates a high amount of illegal bycatch, the fishermen might sometimes opt to dump it—dead—over the side, a process known in the business as discarding. This is a practice that fishery managers find almost impossible to quantify and has often led to significant underestimation of the impact of a fishery.

- Perhaps in the most heinous version of discard, a fishing vessel might make a totally legal catch, reach its quota, but continue to fish in the hopes of catching larger specimens that will fetch a higher market price. If successful, the fisher might discard dead what they already have and restock their hulls with the higher-quality catch. This process is known as high grading; it is illegal, but again very difficult to monitor and quantify.

- Fishing techniques also vary in their impact on the physical environment. Ground trawls, or draggers, tow nets along the seafloor and can often irreparably damage the seafloor, rendering it useless as habitat for future species.

- Dynamite fishing is a common technique used in developing countries where the need for food is prioritized over the need for regulation. It uses explosives to concuss fish and bring them to the surface either dead or confused, a practice that also destroys habitat.



Dynamite fishing

- Cyanide is sometimes used to stun fish, allowing their capture for use in aquaria—but the cyanide is nonselective, affecting many other species. All these destructive methods are justified in the name of profit, with little thought toward sustainability.

- Worldwide, our fisheries—whether they be for smaller species or for megafauna—are in trouble. Many have been overexploited. Some species have become commercially extinct, meaning that it is no longer financially viable to continue to fish for that species. Some commercial extinctions are so extreme that the future of that species is in significant doubt.

Fisheries Management

- How does one decide how many individuals to catch in any one year? Who is responsible for the management of a fishery, especially when the species is caught outside of sovereign waters? In other words, how do we manage the commons of the open ocean?

- The answer to the first question is the science of fisheries management. A relatively new branch of understanding, fisheries science attempts to model population growth as a function of the number of individuals recruited to a fishery through reproduction and the number of deaths, either natural or caused by fishing.

- The mathematics are fairly convoluted and often rely on the concept that a population is best fished when its growth is maximal, at some point before the population size becomes so large that its growth is limited by the availability of the resources it needs. Thus, managers in the past strove to manage a fished population at a level that produced the so-called maximum sustainable yield (MSY).

- Unfortunately, calculating that point was tricky for a number of reasons. It assumed that environmental capacity was constant, which it was not, nor can it ever be. It assumed that the fished population was reacting instantaneously to the level of fishing pressure, which it could not. Thus, small errors quickly compounded into unsustainable levels of fishing. This, coupled with the economic need to provide jobs and income in the short term as a priority over the long-term goal of sustainability, doomed many of our fisheries to failure.

- As a result, many management agencies now prefer to fish at some percentage of what MSY predicts, thus leaving a margin of error. This is known as precautionary management, a wise practice that perhaps is too late in coming.

- We are also learning to consider more than one species at a time. Within a food web, the population dynamics of different species affect each other constantly. So, if we fish species A, which is a predator of species B, then that might mean a boom in species B's numbers because we have reduced a potential source of mortality.

- A boom of species B, in turn, might have an adverse effect on a third species, C, that serves as prey for species B. We are thus moving from single species management to multispecies management, a much more mathematically complex endeavor. Again, this kind of innovation may be too late.

- These problems are compounded when no one nation clearly is responsible for managing a fishery. Technically, no nation owns the international waters beyond the exclusive economic zone, which establish a country's territory at sea, typically out to 200 nautical miles. However, many desirable megavertebrates use these international areas as habitat or at least migrate through those waters. This presents an opportunity to unscrupulous fishing fleets to work unsustainably with little fear of reprisal.

- In reality, many megafauna are "international." They pay no attention to the red lines that humans like to draw on maps. They are much more interested in ecosystem boundaries, and these of course completely ignore human politics. In such cases, the only recourse we have to protect these species is through the process of international treaties and agreements.

- Bringing together signatories from many countries, treaties recognize that to effectively manage a sustainable fishery, signatory nations must collaborate in the management of that species. This is not as easy as it sounds, and most such treaties have come under heavy criticism from conservationists, mostly because they lack enforcement.

- Many say that, as a society, we are now at a critical juncture in how we manage marine biological resources. Our oceans may have already been irrevocably changed. Our preference today for megafaunal species such as tuna, swordfish, and shark, as well as our past exploitation of whales, seals, and other marine mammals may have irreversibly affected our oceans.

- We have created what is known as a trophic cascade: We fish for the most desired, often largest species first, those higher up the trophic ladder. When that becomes commercially extinct, we fish for the next most desirable, a little further down the food web, and so on. Some believe that we are moving toward an ocean with much fewer fish—where unpalatable jellyfish dominate.

- Rather than managing fisheries for short-term gain and profit, we need to think about sustainability. This will require a change in how politicians, government, scientists, and the industry interact.

LECTURE SUPPLEMENTS

Readings

Etchegary, *Empty Nets*.

Gelb, *Jiro Dreams of Sushi*.

Jennings, Kaiser, and Reynolds, *Marine Fisheries Ecology*.

Junger, *The Perfect Storm*.

King, *Fisheries Biology, Assessment and Management*.

Kurlansky, *Cod*.

Liss, Laub, and Abel, *Sacred Cod*.

Murray, *End of the Line*.

Web Resource

Smithsonian Institution, “Ocean Portal: Overfishing,” http://ocean.si.edu/conservation/overfishing.

Questions to Consider

1. What kind of fresh (not canned or bagged) tuna does your local supermarket sell? Research where it comes from and how it is caught. Is that fishery considered sustainable?

2. A good example of an international, transboundary management coalition for a migratory fish is the International Commission for the Conservation of Atlantic Tunas (www.iccat.int). Research this organization to learn what it is doing to conserve Atlantic tuna stocks. Be sure to also look for web links outside of the organization’s website to learn of the criticism of the commission’s management protocols.

3. Research the history of Newfoundland’s northern cod fishery. Identify the key mistakes made in the management of this fishery that caused it to crash.

11

SHARKS AND RAYS

Sharks belong to a taxonomic group known as the chondrichthians, the subject of this lecture. Chondrichthians are divided into 2 groups: the Elasmobranchii; a group that includes the sharks, skates, rays, and sawfish; and the Holocephali, or chimaeras, which are a group of deep-sea-living fishes. This lecture focuses on the elasmobranchs, which can be broken down even further: the Selachii contains all the modern sharks, while the Batoidea contains the rays, skates, and sawfish.

Chondrichthians

- As chondrichthians, all elasmobranchs are also chordates. Being a chordate means having certain characteristics. First, all chordates possess a notochord at some point during their life history, a back-stiffening rod that supports the body form. Chondrichthians only possess a notochord during their embryonic phase. As the embryo develops, the notochord is replaced by a cartilaginous vertebral column.

- Cartilage is a tissue similar to bone, but less rigid and more flexible. However, it still retains sufficient rigidity for it to serve a skeletal function. And because they use cartilage rather than bone for an internal skeleton, we often refer to sharks, skates, and rays as the cartilaginous fish.

- All chordates possess pharyngeal gills, at least in the embryonic phase. In the chondrichthians, these are maintained in the juvenile and adult forms as a way of exchanging respiratory gases with the surrounding water. These organs allow them to extract oxygen from the water and dump unwanted carbon dioxide, a by-product of respiration.

- In the bony fish, the gills are protected by a gill flap, or operculum: however, chondrichthian gills lack this protection. In many species, especially bottom dwellers, water enters in through a small pore behind the eye called a spiracle; this helps the animal pull in clean water rather than breathing in muddy water from the underslung mouth. Pelagic sharks—living in the open water column—do not need this adaptation, so it is minimized.

- Some sharks, such as the whale shark, are incapable of pumping water over the gills as most bony fish can. So, to have access to fresh, oxygenated water, they must constantly swim, continually pushing water over the gills in the same way that air flows

through a jet turbine. If these species stop swimming, they start to act as if drugged because of the lack of an oxygenated circulatory system.

- Compared to the rest of the cartilaginous skeleton, the jaws of sharks have been specially strengthened through calcification. However, the teeth are not embedded in the jaw as they are in land vertebrates. Instead, they are fixed in the gum tissue; if ripped out—which frequently happens—they are replaced by further rows of teeth.

While the 6-meter great white is notorious as a predator, perhaps the fiercest of all the sharks was an animal that is no longer alive. *Carcharocles megalodon*, or just megalodon for short, grew a massive 18 meters—3 times the size of the largest current-day shark predator. Its teeth were the size of human hands, and its mouth was so large that you could have driven a motorcycle through it with room to spare.

- Most shark teeth are razor-sharp, although as with all toothed animal species, the morphology of the tooth reflects the diet that they consume. For example, the teeth of the great white are flattened like a chisel, serrated, and pointed, allowing the shark to rip into flesh and then cut through it as it whips its head from side to side. This makes for a messy wound, and a shark victim often bleeds to death.

The cookiecutter shark is a parasitic dogfish whose teeth are highly modified to create a sawlike ridge that extends around the mouth. In feeding, the shark attaches its mouth to the surface of its typically much larger prey and carves out a disc-shaped chunk of flesh, leaving a very characteristic lesion and scar pattern.

- Some chondrichthians have chosen through natural selection and evolution a life of filter-feeding over predation. Four species—the whale shark, basking shark, megamouth shark, and manta ray—feed exclusively on plankton suspended in the water column. But feeding on tiny plankton does not seem to restrict the size of these animals; the whale shark, the largest fish in existence, can reach perhaps 14 meters.

- Each of these species uses modified gill rakers to catch their prey, and the manta ray even has an extra set of modified fins around the mouth, called cephalic fins, which help direct the flow of the water into the mouth and out by the gills. All of these species still have teeth—much reduced and at this point pretty much nonfunctional.

- In addition to a notochord and gills, a third quality of all chordates is a postanal tail. In the chondrichthians, this has become highly modified, and in the case of the sharks, it has become an extremely powerful propulsion unit that varies morphologically across species.

- In some cases, such as in the great white, the upper and lower lobes of the tail fin approach similar proportions. In most species, though, the upper lobe is considerably larger than the lower lobe, a morphology known as heterocercal, which is thought to improve locomotive efficiency.

- Chondrichthians, unlike their cousins the bony fish, do not possess a swim bladder and therefore cannot regulate their buoyancy in the same way. Some species—sharks, for example—address this issue, in part, by having large livers that contain buoyant oil. However, most of the lift a shark needs comes from swimming and keeping the pectoral fins at a slight upward angle, creating an upthrust in much the same way an airplane wing creates lift when subjected to a flow of air.

The flattened appearance of a ray is not to be confused with bony flatfish, which are laterally flattened and then swim on their side, one eye migrating to the upper side of the fish during post-larval settlement.

It's a wholly different type of morphological adaptation that results in a similar outcome.

Evolutionists would call this a type of convergent evolution, whereby a bottom-dwelling lifestyle has caused the same morphological solution in 2 different evolutionary lines.

◇ Most species of cartilaginous fish are somewhat dorsoventrally flattened, giving them a somewhat squashed appearance in cross-section. This is carried to an extreme in the skates and rays, which appear almost flat in cross-section. The large wings of a ray—in reality, greatly modified pectoral fins—offer up massive surfaces that can be used as a source of propulsion, and the ray's tail may or may not play a role in movement.

◇ Cartilaginous fish also all have a particular kind of fish scale referred to as a dermal denticle, sometimes called dermal teeth, or placoid scales. Shark skin is very rough because of the placoid scales; their shape helps reduce hydrodynamic drag.

◇ The final characteristic that chondrichthians share with other chordates is the dorsal hollow nerve cord. With the development of a nervous system, sharks can efficiently transmit neural signals in both directions. Thus, they can coordinate a rapid and intricate muscular response, allowing them to move rapidly, in a highly maneuverable way, as a predator needs to do. They can also receive and coordinate an array of sensory information.

◇ Most chordates possess a cranium. Members of this clade are called craniates, and all elasmobranchs fall within this group. This is important because the cranium, or skull, can house a brain of significant mass, and that brain, in turn, can process complex sensory information and coordinate intricate body movements.

◇ Sharks are perhaps not known for their intelligence. However, there is a good correlation between predatorial lifestyle and brain size; in essence, one needs a bigger brain to swim faster and more accurately and to coordinate the intricacies of a prey capture.

Sensory Ecology

- Chondrichthian sensory ecology is complex, highly adapted, and unique in its capacity. A shark's ability to sense its environment is extraordinary.

- Shark vision appears to be good, though it's likely not as important as other senses. The eyes are large, to maximize light intake in the murky depths of the ocean. Most evidence suggests that sharks have monochromatic vision; in others words, they see in shades of one color. However, they are extremely good in detecting contrast, which is essential when hunting at night.

- Sharks have an excellent sense of smell and taste, 2 senses that we can group together under the category of chemoreception. One of the sensory cues that sharks are attracted to is the taste of blood in water. Some species of shark can detect that taste at concentrations of one part per million, or perhaps better—that's one tiny drop of blood in 50 liters of water.

- The sense of hearing is tied closely to the sense of vibration, as both sound and vibrations are transmitted as pressure waves. In addition to ears, sharks also possess a lateral line system, an organ seen in most aquatic vertebrates that evolved originally in water. It is a highly sensitive mechanical reception system that can detect minute vibrations in the water. The combination of ears and the lateral line system creates a sensory array that can detect the thrashing of prey thousands of meters away.

- Sharks can also sense electrical currents. This is a sensation that would be lost on humans, as air cannot transmit electrical currents except in extremely high-voltage situations, such as those within a lightning bolt. But water, especially saltwater, transmits electricity very well, and a shark's prey emits an electromagnetic field that is quite detectable.

- ◇ This is because all physical movements involve electrical potentials that are responsible for initiating the contraction of muscle fibers. In fact, we now know that animals produce a detectable electric field even when they're at rest, so imagine the kind of field that a thrashing or panicked prey might emit. Of all animals tested, sharks have proven to be the most sensitive to electromagnetic fields.

- ◇ There might be an added benefit to the ability to detect an electromagnetic field. Fluid conductors, such as seawater, will induce an electric field simply through their movement. Therefore, the ocean currents themselves might create electromagnetic fields that sharks use for orientation during migration.

- ◇ Elasmobranchs, as ancient as they are, have conquered pretty much every niche in the ocean. We find them in neritic and open ocean habitats, distributed pelagically, demersally, and benthically, in all but the deepest of water. With the exception of the filter-feeding group, they are all predators, feeding on prey as large as a marine mammal such as a seal or small dolphin and as small as a crab or mollusk.

- ◇ As predators, they don't have to worry too much about being preyed on themselves; however, there are some notable examples of defense adaptations. For example, stingrays are known for their barbed stinger—a modified scale located about halfway down their tail. The venom it injects is very painful, but rarely fatal to humans, unless the victim has a frail constitution or if the sting causes anaphylactic shock. Luckily, stingrays are very timid and will move away from an encroaching human if given plenty of warning.

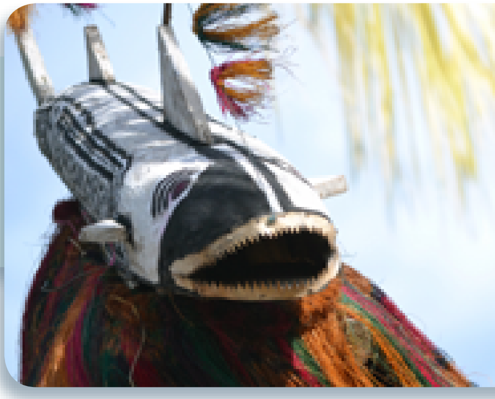
Sharks as Victims

- A staggering number of sharks are killed each year—as part of directed fisheries and as bycatch. Collectively, this number reaches into the tens of millions. Rays and skates are also fished, but not to the same extent. As megavertebrates, elasmobranchs are highly valued in fish markets, and their wide distribution globally means that they are easy to find and catch.

- Similar to tuna, large sharks can be cut into steaks, whereas skates and smaller sharks provide a white-fleshed fillet that is easy to prepare.

- Most elasmobranch fisheries tell the same tale—one of overexploitation that will inevitably lead to commercial extinction. Management and regulation are issues, because many shark species are migratory. Few agreements exist between countries to jointly manage the population, although the United Nations Memorandum of Understanding on the Conservation of Migratory Sharks is a significant step forward.

Some aboriginal cultures, particularly those associated with the ocean, adopted sharks as gods. More recently, people have mostly been interested in this group as a source of food.



- Perhaps the most heinous and unsustainable fishing practice anywhere is the shark finning industry. In this fishery, sharks are caught live. Their dorsal fin is then cut off, and the shark is then returned, bleeding but alive, back to the water. The animal soon dies because it can no longer swim correctly.

- Shark finning is cruel—yet it occurs worldwide and is mostly unregulated. This practice is allowed to continue because the product, shark fin soup, is highly prized on the Asian market as a homeopathic means to improve sexual potency and lower cholesterol. However, in reality there are no scientific data to support such claims. In fact, as apex predators, sharks tend to accumulate toxins, such as mercury, in their flesh. So, eating them consistently over a lifetime may actually be unhealthy.

- ◇ A few countries have made the practice of finning illegal, and other countries ban the import of fins. But black markets persist. And shark populations suffer and decline. Unfortunately, sharks are becoming just another example of an overexploited marine megavertebrate—all because they taste good.

- ◇ They still also suffer the stigma of being killers, in spite of the fact that, in reality, only a few species are known to have killed humans. Most sharks are benign and are actually scared of us. We ought to admire them for being incredible predators with amazing abilities. But instead, the media tends to sensationalize stories of shark attacks, and this only reinforces that killer reputation.

- ◇ The message is slowly getting out to those who are willing to listen. Documentaries these days focus less on the reputation of sharks as killers and place greater emphasis on debunking myths about them. Meanwhile, ecotourism is increasing our exposure to these animals, helping create safe interactions with a range of species.

LECTURE SUPPLEMENTS

Readings

Convention for Migratory Species, "Memorandum of Understanding on the Conservation of Migratory Sharks."

Florida Museum, "International Shark Attack Files."

Klimley, *The Biology of Sharks and Rays*.

Skomal, *The Shark Handbook*.

Web Resources

Smithsonian Institution, "Ocean Portal: Sharks and Rays," http://ocean.si.edu/ocean-life-ecosystems/sharks-rays.

———, "Shark Finning," http://ocean.si.edu/ocean-news/shark-finning-sharks-turned-prey.

Questions to Consider

1. Visit the website of the International Shark Attack File (www.floridamuseum.ufl.edu/fish/isaf/home/) and research the prevalence of fatal shark attacks. Where are the main hot spots? Are shark attacks decreasing or increasing? Which species are believed to be the main perpetrators?

2. Research the United Nations Memorandum of Understanding on the Conservation of Migratory Sharks under the Convention on Migratory Species (http://www.cms.int) and learn what member states are doing to conserve shark species and, in particular, to reduce the practice of finning. Are shark populations increasing?

3. Consider the shark's typically higher position in the food web. From what you learned from the lecture, what adaptations can you list that specifically help the shark be a top predator?

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MARINE REPTILES AND BIRDS

In this lecture, you will learn about 2 specific clades of megafauna: the marine birds and sea turtles. While these 2 groups might initially seem somewhat disparate in nature, they are very closely related—so close that many choose to place birds within the class Reptilia, as we will here. Within Reptilia there are many divisions, but only 2 groups notably retain strong ties to the marine environment: the Chelonioidea, better known as the sea turtles, and the Archosauriformes, which include the crocodiles, dinosaurs, and birds.

Marine Turtles

- The superfamily Chelonioidea, as the common name of sea turtle suggests, contains exclusively marine species, distinguishable from the 320 or so riverine or land turtles and tortoises. There are 7 species: the leatherback, Kemp's ridley, olive ridley, loggerhead, hawksbill, green, and flatback turtles.

- Considered together, marine turtles can be found worldwide, except in the Arctic and Antarctic Oceans. This is likely because marine turtles are ectothermic, meaning that they are cold-blooded, like their ancestors the fish.

Hawksbill (*Eretmochelys imbricata*)

The shell of a sea turtle acts as a sort of defensive shield, protecting the animal's internal organs. However, unlike land turtles and tortoises, sea turtles cannot retract their body fully inside their shell.

- Being ectothermic has benefits and disadvantages. On the plus side, sea turtles do not need to invest energy in staying warm; their physiology is adapted so that they can operate metabolically at the typically low temperatures of the ocean. There are, however, limits to this, as demonstrated by their absence from polar waters, where it is just too cold.

- The main disadvantage to being ectothermic is that because the surrounding environment is relatively cold, the internal temperature of sea turtles is also cold, and this limits their metabolism. In other words, physiological chemistry happens at very slow rates. The turtle's slow metabolism is a potential explanation for why they live so long. Estimates suggest that some species may live longer than 80 years.

- The one exception to this lack of cold tolerance is the leatherback turtle, the largest of all the sea turtles, and one that is so different that we place it in its own family, Dermochelyidae. Leatherbacks are endothermic—that is, like humans, they can maintain a body temperature independent of the surrounding environment. This is doubtless why leatherbacks have the highest latitude distribution of all the sea turtles.

- The most obvious part of a sea turtle is its shell, which has 2 main parts: the carapace, which forms the dorsal portion of the shell, and the plastron, which makes up the ventral portion. Both the carapace and the plastron are further made from scutes, the individual smaller plates that are similar to enlarged bony or hornlike scales; in fact, scutes are very similar in construction to the external covering of bird legs.

- Leatherback turtles, which can grow to almost 2 meters in length and 600 kilograms in weight, have a slightly different type of shell. A leatherback's carapace is covered by a layer of skin and flesh, and it lacks an essential form of keratin that would otherwise harden its shell.

- As the shell is living material, to an extent a turtle can repair its shell if it has been compromised. Also, a turtle's health can often be diagnosed through the condition of its shell.

- As diving animals, sea turtles face many of the same challenges that whales and other marine mammals have had to overcome. Similar to mammals, they must hold their breath when diving; gills went out with the fishes, and reptiles possess lungs that are incapable of extracting oxygen efficiently from water. In a turtle, the lungs are located dorsally and likely aid in the animal's buoyancy.

How long a turtle can stay underwater is a function of its activity. An actively foraging turtle may be down for 10 minutes—an impressive feat in itself—but a sleeping turtle can stay down for hours.

- As one might expect, sea turtles are well adapted to the marine environment. They are strong swimmers, using a form of modified breast stroke, with the power coming mainly from the front flippers. For the most part, they have broad omnivorous diets; they are not especially fast, so they essentially eat what they can catch. Again, the leatherback is the exception here: It feeds almost exclusively on jellyfish and, in some cases, has developed complete immunity to a jellyfish's sting.

- We know little else of turtle life history because they spend so much of their time in the vast open ocean. We've obtained most of our knowledge by observing them when they come inshore to lay eggs on sandy, secluded beaches or when they wash up dead or moribund.

Threats to Sea Turtles

- Almost all turtle species are listed either as endangered or vulnerable, mostly because of a bloody and exploitative history with humans. We have hunted some species mercilessly for food and for the shell.

- As a society, we also threaten sea turtle sustainability in other incidental ways. Because they hunt mostly at or close to the surface, they often get caught in fishing nets and risk being drowned, and few have the strength to survive.

- Trawls and dredges can often uncover turtles on the seafloor, damaging the carapace; to some extent, this issue can be mitigated by creating an escapement window in the net known as a turtle excluder device. Sometimes a boat's propeller will cut into the shell when the animal is floating invisible just below the surface, fatally ripping into the lungs.

- But perhaps the most insidious impact we have on turtle populations is on their nesting habitat. Sea turtles must come to shore to lay their eggs, burying them in nests less than a meter deep on a sandy beach, away from predators such as birds, coyotes, and foxes.

- However, humans like sandy beaches, too, and therefore often compete for the same habitat. Noisy condominiums and hotels with bright lights at night will often deter the turtles from nesting; if the female parent does decide to nest, the hatchlings might be more attracted to the lights of the human habitation, delaying their journey to the relative safety of the open ocean and thus exposing themselves to predation from seabirds and land predators.

- All these threats that sea turtles face are compounded by the fact that, compared to other species, we know so little about them. But technology for monitoring species at sea is improving, and over time this will give us a fuller picture of how these marvelous creatures live. That’s important for the turtles themselves because, as with most conservation issues, progress begins with awareness and education.

Seabirds

- The birds are a diverse group of winged tetrapods. Birds evolved from reptilian ancestors, with the reptile's scales believed to be preadaptations for feathers. All birds are endotherms and thus have a greater degree of thermal tolerance. For this reason, we see a broader distribution of marine bird species around the globe, penetrating into the polar regions.

- Within the group Aves, there are a number of orders, which are further divided into families. With a few exceptions, none of these families is exclusively marine.

- Some birds, such as ducks and various waders, stay very close inshore, perhaps only using the intertidal areas, and only fly over the ocean to get to another beach; their dependence on the marine environment is therefore restricted to nutritional needs.

- At the next level of investment are birds that demonstrate much more complete adaptation to the marine environment, and it's on this group that we will focus. They include a wide variety of families and species, ranging from penguins to puffins, from neritic gulls to gannets, from petrels to pelicans, and many more.

- All of these species have adapted to life on and around the ocean. But that's not to say that they've all adapted the same way. Because, in fact, there's extraordinary diversity in the behaviors they depend on for survival.

Northern gannet (*Morus bassanus*)

- ◇ Take feeding behavior, for example. Some seabirds barely dive into the first few centimeters of the ocean. Terns, fulmar, gulls, and petrels, for example, do not dive deep; instead, they take prey from the surface of the ocean either while flying above or floating on the water's surface.

- ◇ But then there are plunge divers, such as gannets, which spot their prey from high above, tuck their wings tight to their body, and dive arrow-like into the water, using the impact of their dive to reach depths of 10 meters.

- ◇ Still other species are pursuit divers. Penguins are probably the best example of this group. Their amazing swimming ability allows them to chase prey underwater, reaching speeds of 12 kilometers per hour. Pursuit divers dive from the surface—rather than from the air—relying on breath holding so that they can stay underwater for extended periods of time. Other examples of pursuit divers include the auks, shearwaters, and albatrosses.

- ◇ Some seabirds are carrion eaters, and perhaps no marine bird represents this group better than the giant petrel, which reaches a wingspan of more than 2 meters and a body weight of almost 10 kilograms. They often immerse their entire head into a bloody carcass of a seal, sea lion, or penguin to rip out a piece of flesh.

- ◇ Some bird species, such as the skuas, will attack live prey on land, such as a seal pup or penguin chick. Shaped rather like a gull, only darker in color with a hooked beak, skuas are a serious threat to penguin colonies.

- ◇ The final feeding strategy seen in the marine birds is to wait for other birds to catch the prey and then to steal it from them. This is called kleptoparasitism, and it's seen particularly often in the skuas, jaegers, and gulls.

◇ For humans, drinking seawater leads to greater dehydration than drinking freshwater, because the salt causes us to push more water out of our blood and lose it through our urine. Many seabirds can drink seawater; they simply have physiological pathways within their bodies to exclude the salt.

◇ While we often associate birds with the ability to fly, in fact not all do. Notably within the marine birds, the penguins are flightless, as was a recently extinct alcid species known as the great auk. However, wings are not vestigial in these flightless species; rather, they are used to paddle through the water during a dive.

Some of the larger penguin species, such as the emperor penguin, can dive to extraordinary depths—more than 500 meters—for up to 20 minutes.

- Other strong swimmers, such as the puffin and other auks, retain the ability to fly, but they don't do it with the grace of many of the other seabird species, because they, too, have taken the evolutionary compromise and modified their wings for underwater swimming ability.

- Many pelagic birds will spend days and weeks on the wing at sea, traveling vast distances. Perhaps the most legendary flyers are the albatrosses. This group contains the largest flighted bird: the wandering albatross, at a wingspan of more than 3 meters.

Albatrosses are superb fliers, using a kind of flying known as dynamic soaring, in which the albatross swoops down toward the water, pulls up at the last minute, and uses the energy from its dive, coupled with updrafts caused by waves, to push itself back up high before it then commits to its next swoop. Up and down, bending left then right, in a zigzag pattern, they can do this for hours without ever flapping their wings.

Population Status of Marine Birds

◇ Many bird species, and their eggs, have been hunted either as a source of food or for their feathers. This practice has gone on for hundreds of years. For some species, it was unsustainable. For example, the great auk, an easy-to-catch flightless species, is now extinct because sailors favored it as a source of fresh food that could help combat scurvy. Certain other species are hunted still—such as the murre of maritime Canada—but with stricter regulations that many believe create a sustainable hunt.

◇ The main concerns for marine bird populations today are subtler, but still significant. As predators at the top of their food chain, they risk bioaccumulation of various pollutants that are dumped into the ocean. They inadvertently eat nonbiodegradable plastics that in themselves might have absorbed a number of toxic pollutants. They are also susceptible to oil spills; oil will mat and weigh down their feathers, making flight impossible. Oil ingested during preening can poison the animal.

◇ Seabirds are particularly vulnerable in their breeding colonies, where they can be very densely packed together: Many species gather annually in the hundreds of thousands to breed at very specific sites. The accidental introduction of a land-based predator such as dogs, foxes, feral cats, or rats can have devastating effects on these colonies.

◇ A final concern is that fishing gear will often incidentally take marine birds as bycatch. While there are clear cases of birds trying to steal fishing bait, most bycatch appears to occur because humans and seabirds fish in the same areas, sometimes for the same species. In fact, fishermen sometimes rely on seabirds to help them find fish.

LECTURE SUPPLEMENTS

Readings

Coleridge, *The Rime of the Ancient Mariner.*

Enticott, *Seabirds of the World.*

Safina, *Eye of the Albatross.*

————, *Voyage of the Turtle.*

Schreiber and Burger, *Biology of Marine Birds.*

Spotila, *Sea Turtles.*

Web Resources

Smithsonian Institution, "Ocean Portal: Birds," http://ocean.si.edu/ocean-life-ecosystems/birds.

————, "Ocean Portal: Reptiles," http://ocean.si.edu/ocean-life-ecosystems/reptiles.

Questions to Consider

1. Why specifically does the strategy of amniotic oviparity provide independence from an in-water existence? How might it lead to a more altricial strategy in parenting?

2. What common features have led scientists to place the clade Aves within Reptilia?

3. In terms of evolutionary development, where do feathers come from? What do scientists believe was their original function? (Hint: It wasn't flight!)

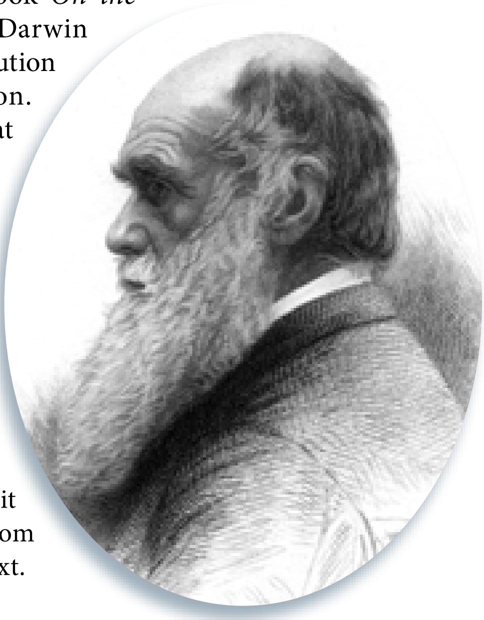
13

THE EVOLUTIONARY HISTORY OF WHALES

This lecture will introduce you to the final group of marine megavertebrates—the marine mammals—a group that will be examined in detail over the next several lectures. This lecture will lay the foundation by examining the evolutionary history of marine mammals. Within the class Mammalia, we can now track 5 separate lineages of marine mammals, each representing a separate return from the land to the water. Given this complexity, the lecture will focus on the example of whale evolution: how whales, or cetaceans, evolved from land-dwelling animals into the aquatically adapted species we know today.

Evolution through Natural Selection

◇ In his groundbreaking book *On the Origin of Species*, Charles Darwin develops his theory of evolution through natural selection. The modern version of that theory can be summarized by focusing on 4 key principles that build on one another.



1. We can observe that within a species, there is individual variation.
2. We know that this variability is heritable—it can be passed down from one generation to the next.
3. Resources are limited; therefore, there will be competition between individuals.
4. Among all the individual variants, some will have a competitive advantage over others and will therefore stand a higher chance of reproductive success.

◇ The result of this is that traits that provide a competitive advantage will be "naturally" selected and passed on to future generations. Here, the term "natural" means that it occurs in nature, and distinguishes it from artificial selection, in which we deliberately breed animals for specific traits. But the essence of evolution by natural selection is this: Individuals will have differential reproductive success based on traits that can be inherited.

- When Darwin developed his theory of natural selection, islands played an important role in his insights. Doing his research in the Galapagos Islands, he compared the fauna and flora of the different islands. And he began to think about how seemingly different species, geographically close yet isolated, appeared to have unique adaptations specific to the environment of the island on which they lived. This is because islands provide an isolating mechanism.

- Imagine, on a larger scale, a continent inhabited by a particular species that is homogenously distributed throughout the land. The continent is small enough, and the species is mobile enough, that all the individuals of this species have an equal chance of breeding with each other. So, the genetic makeup of this species is pretty uniform throughout the continent because everyone is breeding with everyone. Importantly, this species cannot swim.

- Through the process of plate tectonics, let's break up that continent into 2 pieces. We just created 2 isolated populations of the same species. Through continental drift, one continent, called A, over millions of years drifts toward the equator; the other, called B, moves to a more polar distribution.

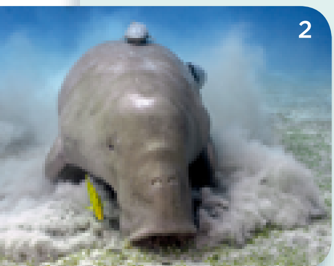
- The organisms on continent A start, over geological time, to experience a more tropical climate. So, there is selection pressure for adaptations suited to that kind of environment. The organisms on continent B go through a similar kind of selection pressure but for adaptations that favor a more polar climate.

- Slowly, the 2 populations drift apart—not just geographically, but also genetically because they cannot interbreed due to the geographic isolation. If the genetic drift causes the 2 populations to become so different that they can no longer interbreed, we call them 2 separate species.

- This is a classic case of what is known as allopatric speciation, whereby some geographical boundary prevents 2 populations from interbreeding, and thus they speciate. This is distinct from sympatric speciation, in which no geographical barrier is needed; rather, there is behavioral isolation between subspecies.

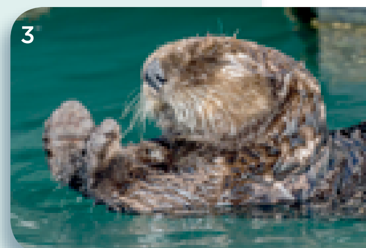
- Natural selection works on individuals; it's the individual that either survives or doesn't survive. However, evolution works on populations by shifting the proportion of gene expression in favor of genes that are adaptive to an environment. Small changes over large geological-scale periods of time lead to substantial changes and speciation.

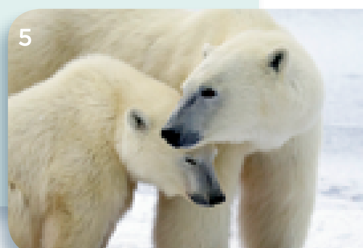
Within the class Mammalia, we can now track 5 separate lineages of marine mammals.



1. Whales, dolphins, and porpoises belong to an order known as the Cetartiodactyla.
2. Dugongs and manatees belong to the order Sirenia.
3. Sea otters belong to the family Mustelidae.
4. Seals, sea lions, and walruses belong to the suborder Pinnipedia.
5. The polar bear belongs to the family Ursidae.

The closest related of these 5 groups are the last 3 families, which fall under the order Carnivora.





The Evolution of Whales

- The first whales did not look much like whales. They were 4-legged land dwellers, known as the archaeocetes, a name that translates as "ancient whales." These land-dwelling archaeocetes lived in the Eocene epoch, a geological time period that lasted from 56 to 34 million years ago.

- The Eocene is the middle epoch of the Paleogene period, an era that began with the famous Cretaceous-Paleogene extinction, or K-P extinction, which occurred about 65 million years ago. This catastrophic event is believed to have been the result of a large asteroid that impacted our planet, causing a global dust cloud as well as high levels of volcanic and seismic activity.

- The darkening of our atmosphere blotted out the Sun, sending the planet into a winter that lasted for possibly thousands of years. As a result, 75% of species alive on the planet at that point became extinct, including the highly successful dinosaurs that could not adapt quickly enough to the plummeting temperatures and the lack of food caused by the reduction in available photosynthesis.

- However, a new class of animals survived this extinction—the mammals, at the time quite mouselike or shrewlike. Importantly, mammals were endothermic. With the exception of the birds, most of the animals we have explored up to this point—either on oceans or on land—were ectotherms.

- Ectotherms conform their body temperature to the current ambient temperature. And because metabolic activity is temperature dependent, ectotherms have a very real lower limit in temperature tolerance. If too cold, the animal simply cannot survive.

- Endotherms employ a different strategy. They use the heat generated though cellular respiration to maintain their body temperatures at a point that is optimal for peak efficiency in metabolic activity. They often have insulating structures—such as feather, down, fur, and fat—that stop them from losing that heat to the environment.

- This allows endotherms, to a degree, to be somewhat independent of environmental temperature. Thus, the early mammals, as endotherms, could survive the frigid temperatures that followed the K-P extinction, living mostly on insects.

- In the first epoch of the Paleogene, called the Paleocene, mammals quickly became very successful and grew in stature, filling in the ecological niches that had been formerly occupied by the dinosaurs. Then came the Eocene, the second epoch of the Paleogene.

- The fossil record for whale evolution is full of missing links. However, we have captured what we now believe to be one of the first, if not the first, archaeocete. This oldest of the archaeocetes dates back to the boundary between the Paleocene and Eocene, a time when one of the dominant oceans was the Tethys Sea.

- The Atlantic Ocean at this point was still relatively young, and India had yet to collide with Asia. Little remains of this ocean basin today, but one can imagine the Tethys occupying areas of the western Pacific, Indian Ocean, and Mediterranean. Thus, the countries of the Middle East, especially Pakistan, are now ancient uplifted shorelines of what was then the Tethys Sea.

- So, our first archaeocete whale was in fact discovered nowhere near the modern-day ocean, but along an ancient shoreline of sandstone-rich sediments in Pakistan. It was named *Pakicetus*, which translates as "whale of Pakistan." *Pakicetus* looked nothing like a whale; it was a quadruped, somewhere around the size of a wolf.

- Its dentition suggests that it was a fish eater, and therefore probably hunted in the intertidal or riverine and estuarine environments. We think that at the time, mammals were so successful that the competition for food on land was quite intense. Yet the intertidal and shore areas were niches yet to be exploited, so the various species of *Pakicetus* radiated into those areas.

- Traditionally, we had believed that archaeocetes evolved from a group known as the mesonychians, a now-extinct group of primitive omnivorous mammals. However, there is a founding principle in taxonomy that states that if 2 organisms look alike in terms of their morphology and anatomy, then they are more likely to be related to each other than 2 organisms that appear dissimilar. This principle is called homology.

Pakicetus

◇ When researchers used homology to compare fossilized ankle and shinbones of archaeocetes, they discovered that the closest relatives of whales were, in fact, the artiodactyls, or even-toed ungulates, such as the giraffe, hippopotamus, and camels. In fact, we are now so sure of this link that we have renamed the clade that includes all of these creatures as Cetartiodactyla.

◇ *Pakicetus* was clearly a land dweller that occasionally dipped into the waters of the Tethys. Its spine, pelvis, and limb structure were all designed for running. Its vision was binocular, facing forward; its ears were designed for hearing in air, and its nostrils were at the tip of its snout. However, as *Pakicetus* began to forage farther and farther into the shallow waters of the Tethys, natural selection started to play its hand.

◇ A few million years later, we start to see evidence of a new genus of archaeocetes, known as *Ambulocetus*, or "whale that walks." Fossils of *Ambulocetus* were first discovered also in Pakistan, indicating the importance of the Tethys Sea in the evolution of archaeocetes.

◇ *Ambulocetus* did not evolve from *Pakicetus*; it seems more likely that they shared a common ancestor. However, it was clearly better adapted to an ocean habitat. It was the size of a large modern-day seal, and it probably swam using side-to-side tail movements as well as hind-limb paddling, similar to today's otter.

◇ These kinds of adaptations would have made it less mobile on land. Importantly, the ear bone of *Ambulocetus* shows the beginnings of adaptation to in-water hearing; because air and water transmit sound at different efficiencies, an ear designed to work in water has to be more substantial. Also, the nostrils, or nares, of the animal were placed farther back on the snout, presumably to help the animal take a breath without having to lift its head too far out of the water.

> It has taken about 60 million years for the polyphyletic marine mammals to reach the diversity of animals we see today.

- The remingtonocetids were a dominant group of archaeocetes about 45 million years ago. The movement toward a fully aquatic existence is even more apparent at this point. Our knowledge of these species is based mostly on skulls, although it is clear that the animal was still a quadruped, with a few fossils demonstrating the presence of a pelvis and clavicle structure designed to bear weight. The skull was even more elongated at this time, and the ears show further adaptation to hearing underwater. But they were still quadrupeds, and therefore we propose that they were still tied to land.

- The protocetids rose to dominance a few million years later and included genera such as *Rodhocetus*, *Dorudon*, and *Maiacetus*. Dependence on land was still clear. However, the aquatic adaptations were even greater by this point. The nares had migrated to about halfway down the rostrum, which was more elongated due to extension of the cranial bones—a process referred to as telescoping. Also, the pelvis seemed less important as a weight transference structure. All of this indicates that by around 35 million years ago, archaeocetes were starting to lose their land dependence.

- *Basilosaurus* was around until about 34 million years ago, roughly the end of the Eocene. *Basilosaurus*—the last of the archaeocetes—was a magnificent creature, measuring 16 meters in length, much bigger than any prehistoric whale that had come before.

- By now, cetaceans were fully independent of the land. It is difficult to say when exactly whales developed dorsoventral oscillation of the flukes as a swimming method, but by the time we get to *Basilosaurus*, it appears to be in place—or at least an early form of fluking. The structure of *Basilosaurus*'s vertebrae indicate an almost eellike movement, but up and down rather than side to side.

- Its forelimbs had now flattened to become flippers, and although it still had hind limbs, they probably had little function other than to help the animal walk along the seafloor. The nares of *Basilosaurus* were positioned even farther back, allowing the animal to take a breath without raising its head above the surface. Its hearing was clearly adapted for underwater.

You can find a rare example of *Basilosaurus*, the last of the archaeocetes, at the Smithsonian National Museum of Natural History in Washington DC.

Basilosaurus is now considered one of the first fully aquatic cetaceans, part of a larger group that is referred to as the marine mammals.

- In the Oligocene, the epoch that follows the Eocene, we find the dawn of the Neoceti. Up to this point, all prehistoric whales had been toothed. However, in the Oligocene, a group of whales began to grow baleen, an alternative structure for prey acquisition that allowed the animal to filter the water for smaller prey items, such as plankton.

- A key fossilized species, called *Aetiocetus*, shows that their skulls possessed both teeth as well as the preadaptations for baleen. These species were the first of the baleen whales, or mysticetes. It is from these species that we believe all modern baleen whales—who eventually lost their teeth but kept their baleen—derive. Among these modern mysticetes are the humpback whale and the blue whale.

- The remaining toothed whale species went on to form the odontocetes, the toothed whales, which include modern dolphins and sperm whales.

- We believe that cetacean echolocation also evolved in the Oligocene around this time, although it is difficult to determine if the toothed ancestors of baleen whales could also echolocate. One of the first species we believe to be capable of echolocation was *Squalodon*. Echolocation would then go on to become a mainstay of the odontocetes.

- Both the Oligocene and the subsequent Miocene saw a radiation of cetacean species: Some lines did not succeed and became extinct; others flourished to become the diversity of species we see today.

LECTURE SUPPLEMENTS

Readings

Berta, Sumich, and Kovacs, *Marine Mammals*.

Folkens, Reeves, Stewart, Clapham, and Powell, *Guide to Marine Mammals of the World*.

Jefferson, Webber, and Pitman, *Marine Mammals of the World*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Thewissen, *The Walking Whales*.

Thewissen, ed., *The Emergence of Whales*.

Zimmer, *At the Water's Edge*.

Questions to Consider

1. This lecture focuses specifically on the evolution of cetaceans, only 1 of the 5 representative marine mammal groups. Choose another group (from the remaining pinnipeds, sirenians, marine otters, and polar bears) and review how they are thought to have evolved.

2. Review how the planet has changed tectonically is the past 60 million years. What oceans have disappeared? What oceans have been created?

3. One way to determine the degree of a prehistoric organism's adaptation to water is to examine the ear bones, if the fossil record permits. Specifically, what features do scientists look for to determine if an ear is aquatically, rather than terrestrially, adapted?

14

THE TAXONOMY OF MARINE MAMMALS

This lecture will explore the amazing world of marine mammals, starting with the taxonomic structure of the group and the diversity of forms that exist within it. Specifically, the lecture will address the 5 polyphyletic clades of marine mammals. You will become familiar with some of the species within 2 of these clades: the cetaceans and the pinnipeds.

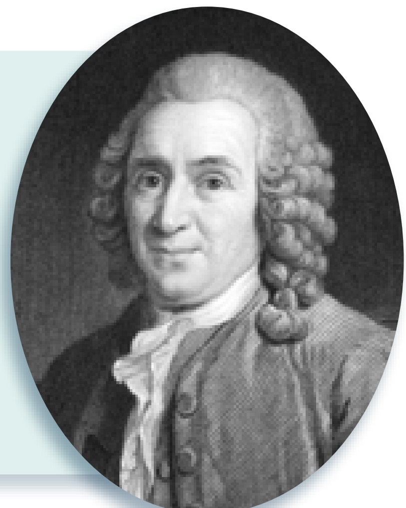
Marine Mammals

- All marine mammals are, indeed, mammals—that is, they derive (as humans do) from the class Mammalia, a vertebrate group found within the phylum Chordata, within the kingdom Animalia and domain Eukarya.

- All mammals share common traits: They possess particularly well-developed brains with a neocortex that is associated with higher brain functions. All mammals are amniotic—that is, they develop their young within amniotic sacs that are typically internalized to the body and fed by a placenta. Most give birth to live young, a condition called viviparity.

- Mammals are endothermic, which means that they are capable of generating their own heat. They possess hair, although the amount might vary significantly, and they have mammary glands, which are used to nurse their young. Most mammalian reproductive strategies are highly altricial, meaning that the parents place relatively lengthy, high-level investment in relatively few young.

When it comes to the taxonomy of organisms, classification schemes are constantly changing. Most of our current classification is based on a system designed by Carl Linnaeus in the 1700s. With the advent of the molecular age and our ability to look at an organism's DNA, we can now perform classification with a much higher degree of resolution. For this reason, we have started to revise the old classification schemes. For the most up-to-date schemes, consult the Society for Marine Mammalogy's Committee on Taxonomy.



- Surprisingly, not all marine mammals are entirely marine. Some are not completely aquatic and spend some time on land. And then there are a small number of freshwater cetaceans and seals. However, because the semiaquatic species still depend on the marine environment, and because the few that depend entirely on a freshwater environment are so similar to their marine cousins, it's safe to call the entire group marine mammals.

- We currently recognize 5 different clades of marine mammals.

  1. Whales, dolphins, and porpoises are part of the clade named Cetacea. Cetaceans spend their entire time in the water and thus live a fully aquatic existence.

  2. The pinnipeds include the seals, sea lions, and walrus and have a semiaquatic lifestyle.

  3. The sirenians include the manatees and the dugongs, and their lifestyle is fully aquatic.

  4. The marine otters derive from the family Mustelidae, or weasels, and while there are several species of otter, only 2 are considered marine: the sea otter and the marine otter.

  5. Representing the ursids, the polar bear is so reliant on the marine environment that is considered to be a marine mammal.

- These 5 groups have very little in common, other than that they are marine and mammals. Cetacea derive from a taxonomic group called the Cetartiodactyla, a relatively new classification that groups them together with even-toed ungulates, such as giraffes, hippopotamuses, and camels. Pinnipeds, otters, and polar bears derive from various arms of the order Carnivora, and the sirenians' closest relatives are the elephants.

◇ Each of these clades represents a separate reinvasion to the aquatic realm after a terrestrial existence for millions of years. So, when we refer to marine mammals as a group, we're using what is called a polyphyletic grouping. This means that the various clades within the group come from separate origins, and while the individual clades are certainly all mammals, they are not necessarily closely related. In other words, there is no one phylogenetic origin to the marine mammals.

◇ However, species in different clades can certainly look very similar. For example, compare the streamlined nature of dolphins and seals. This is an example of convergent evolution. Essentially, this occurs because the environment imposes similar selection pressures on evolving populations of organisms. For example, water is a relatively viscous fluid compared to air, so it makes sense that any evolving marine mammal, independent of which clade it comes from, would tend toward a more streamlined shape as it becomes more dependent on the aquatic realm.

Cetaceans

◇ Within the cetaceans, there is one major division that splits the group into 2: the mysticetes, or baleen whales, and the odontocetes, or toothed whales.

◇ Baleen is a keratinous substance that has a texture very similar to plastic. It is organized into a series of plates that hang from the roof of the mouth of the whale in 2 rows, one for each side of the animal. These become the filtering mechanism for the whale, which eats mostly very small prey that number in the thousands per whale mouthful. The feeding morphology for a baleen whale is not found in any other cetacean species.

- The mysticetes are often referred to as the great whales, a reference to their size, because even the smallest of the mysticetes is relatively big for a mammal, and the largest of them is absolutely huge. However, there is also a species of odontocete that is included in this group because of its size, so while it is true that all baleen whales are great whales, not all great whales have baleen.

- Within the mysticetes are 4 families—Balaenidae, Neobalaenidae, Eschrichtiidae, and Balaenopteridae—containing 14 recognized species.

  1. The Balaenidae, or right whales, includes the bowhead, North Pacific, North Atlantic, and Southern right whale. These are all very stocky, large animals in the order of 15 meters or greater when fully grown. They tend to be better adapted to more polar climes, and their enormous mouth is formed by arched jawbones and rostrum (the part of the skull that forms the upper part of the mouth). Right whales do not possess dorsal fins, and they are typically very slow swimmers.

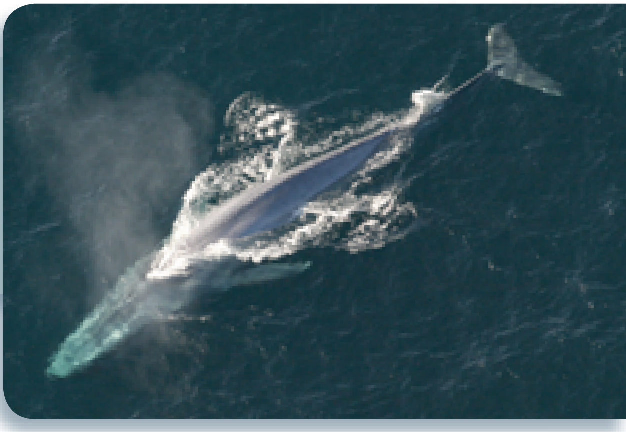
Bowhead (*Balaena mysticetus*)

2 The family Neobalaenidae contains only one species—the pygmy right whale—which, in spite of its name, does not share many of the external features of its larger cousins. It is the smallest of all baleen whales, reaching only 6 meters in length, which is still pretty large for a mammal.

3 Eschrictiidae only contains one extant species, the gray whale. While this species once occupied both the Pacific and Atlantic basins, today it can only be found in the Pacific. Gray whales are relatively large, growing up to 14 meters or so, and unlike other baleen whales, it feeds mostly by sifting through the muds of the seafloor for various crustaceans.

4 The Balaenopteridae is the largest of the baleen whale families, containing 8 species that are sometimes referred to as rorquals. This family includes the humpback whale, blue whale, fin whale, and at least 2 species of minke whale. Rorquals are easily recognizable as being fairly sleek, fast whales; the exception to this is the humpback whale, which is much stockier. All rorquals have dorsal fins, and all have a series of ventral pleats around the area of the throat that allows the floor of the mouth to expand when taking a gulp of prey.

The Balaenopteridae family is home to the largest animal that has ever lived: the blue whale, clocking in at 30 meters and more than 170,000 kilograms.



- All mysticetes filter-feed using their baleen. Because the organisms they take are often tiny—zooplankton, such as krill or copepods—they must process thousands of gallons of water every day. Each baleen whale family has designed a slightly different way to do this.

- The right whales, for example, have an enormous mouth as provided by their arched mandibles and rostrum. They often will feed through the strategy of skimming, whereby they will swim through a patch of prey with their mouth constantly open.

- Rorquals eat similar-sized but faster prey, which they have to chase. It would be inefficient to keep their mouth open in the same way that a right whale does all the time, so they keep it closed, streamlining the body until it is time to lunge and overtake their prey. In that moment, the ventral pleats can expand, giving the whale the mouth volume it needs to gulp the prey.

- Gray whales fall between these 2 in their feeding techniques: They have a few ventral pleats, so their mouth can expand some, as needed. But for the most part, they are sieving the sediment through their baleen, hoping to catch crustaceans that live in the mud.

- The 3 feeding techniques—skimming, gulping, and sieving—neatly separate out the different families on the basis of their differing morphology.

- The odontocetes, or toothed whales, contains 10 families, including the sperm whale, the Kogiidae, the beaked whales, 4 families of river dolphins, the monodonts, the dolphins, and the porpoises. The morphology in this group is highly diverse, representing an expansion of this group into a wide variety of habitats over evolutionary time.

The odontocete group contains the largest dolphin, which is the killer whale, or orca.

Pinnipeds

◇ The pinnipeds include 3 main families—Phocidae, Otariidae, and Odobenidae—so the classification is a little simpler than that of the cetaceans.

1 The phocids are also known as true seals, or sometimes earless seals. Although these animals are semiaquatic, they are better adapted to the aquatic than they are to the terrestrial environment. They are strong swimmers, using their hind flippers in a back-and-forth, sinusoidal motion, powered by excellent back muscles. On land, they are reduced to dragging themselves around using their fore flippers and by a shrugging motion that derives from their back and abdominal muscles. Although they have ears, they do not have external earflaps, or pinna; instead, they simply have a hole in the skin leading to the auditory canal. In this group are 18 extant species that are found in a diverse array of habitats.

The largest phocid is the southern elephant seal. The males weigh up to a crushing 4000 kilograms and measure more than 6 meters in length.

2 The common name for the otariids is the sea lions, which look similar to seals but are better adapted to a terrestrial existence. Perhaps the biggest difference is the sea lion's ability on land to push itself up on its forelimbs and tuck its hind limbs under its pelvis. Phocids cannot do this. As a result, sea lions can achieve a kind of walking gait by lifting their body off the ground. In water, sea lions use their forelimbs to swim, in a modified breast stroke that is extremely effective. Sea lions have earflaps, or pinna, another evolutionary nod to the fact that perhaps these animals are more terrestrial, rather than aquatically adapted. Included in the otariids group are various southern fur seal species that were valued for their fur by early whalers and sealers, as well as other common species, such as the California sea lion and the Steller's sea lion.

California sea lion (*Zalophus californianus*)

3 The odobenids include the walruses, which are found exclusively in the Arctic. And while there is only one species in this family, there are at least 2 subspecies, one for each of the Pacific and Atlantic sides. These large animals approach but don't quite match the size of elephant seals, clocking in at around 2000 kilograms. They were the subject of heavy hunting pressure, mostly for their meat, blubber, and tusks, and their numbers became much reduced. Recent protection has helped the populations rebound a little.

Walrus (*Odobenus rosmarus*)

For every common name of a species, there is also a Latin name, which, at its tightest resolution, takes on a binomial nomenclature: a genus name followed by a species name. For example, the humpback whale's Latin name is *Megaptera novaeangliae*. The binomial description is unambiguous, while common names can often be confusing. The Latin name should be used whenever describing a species scientifically.

LECTURE SUPPLEMENTS

Readings

Folkens, Reeves, Stewart, Clapham, and Powell, *Guide to Marine Mammals of the World*.

Jefferson, Webber, and Pitman, *Marine Mammals of the World*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Reynolds III and Rommel, eds., *Biology of Marine Mammals*.

Web Resource

Smithsonian Institution, "Ocean Portal: Mammals," http://ocean.si.edu/ocean-life-ecosystems/mammals.

Questions to Consider

1. How might the type of prey a right whale feeds on and the habitat in which it lives be linked to the fact that this species does possess a dorsal fin?
2. Review how we believe baleen whales may have evolved from a toothed whale ancestor.
3. Beaked whales surely represent some of the strangest species of all cetaceans. Review this group, paying particular attention to tooth structure.
4. Why is a fur seal in reality a sea lion, and what is the etymology of its name?
5. What is the difference between a manatee and a dugong (both members of the order Sirenia)?

15

HOW ANIMALS ADAPT TO OCEAN TEMPERATURES

Humans are not adapted to live in the ocean, yet the oceans host a group of mammals with similar body core temperatures to humans that seem quite impervious to the cold. How do they get away with this? To answer this question, this lecture will invoke the process of evolution through natural selection, the process that scientists believe can be used to explain adaptation to the environment.

From Fur to Blubber

- The first marine mammals, who lived 65 million years ago, were called archeocetes, or "ancient whales." The first archeocetes were land-adapted dwellers, and as mammals, they retained a fur coat. Fur coats are common in other marine mammal clades—for example, the seals and sea lions, or collectively, the pinnipeds. But the descendants of the archeocetes—whales and dolphins—did not retain their fur, even though they are mammals.

- Fur provides a warming barrier to cold air temperatures by trapping air in small compartments. The denser the fur, the more compartments. Air is wonderfully insulating, so it's not so much that a fur coat makes you warm; instead, it keeps the heat that you have generated as a warm-blooded mammal from being radiated out and lost to the environment.

- Because fur works on the principle of trapping insulating air, it's a great way of staying warm if you intend to stay on dry land. But if your lifestyle requires part- or full-time immersion in water, it's not going to work, for 2 reasons: Fur is very heavy when water laden and therefore becomes a significant source of drag against a swimming animal; and the pressure of water will squeeze insulating air out of those compartments, flattening and crushing the fur so that the cold-water interface is much closer to the skin.

- The king penguin, a cold-adapted organism, can be found in the subantarctic waters of South Georgia. Penguins are not mammals and do not possess fur, but they do have a dense plumage of feathers that can act in much the same way, trapping air that insulates from heat loss.

- In fact, we can use the air-trapping properties of down, feathers, and fur as an example of convergent evolution, whereby an environmental challenge common to various species has prompted, through natural selection, a common solution, albeit using different body structures.

- When a penguin dives, darting to and fro under the water, it emits a trail of bubbles. This is not some artifact of a hidden propulsion system, but simply the trapped air being squeezed out of the feathers by the pressure of the water. The minute the penguin enters the water, to an extent the clock is ticking, although penguins have other ways of staying warm.

- On land, the air trapped in the penguin's feathers acts as an insulator. This is particularly important for chicks, who are somewhat lacking in the internal layers of fat they need to stay warm.

King penguin chicks are sometimes fondly referred to as oakum boys. Their golden-colored down is so fluffy that they resemble the ship's boys of old, who, in tamping the deck with oakum, often seemed to get more of it on themselves than in the cracks between the ship's planks. In fact, the chick's down is so thick that from a distance, it looks like fur.

- The key, whether it be fur or feathers, is that the air trapped inside that gives the coat "loft." Once the animal becomes wet and the air is pushed out, that loft is lost, so the animal must rely on other ways to stay warm until it leaves the water and dries out. Often, semiaquatic animals that depend on a lofty coat of feathers or fur will immediately start preening or grooming once they leave the water, to regain some of that loft.

- Fur is not a good adaptation to rely on as an animal evolves to a more fully aquatic lifestyle. The pinnipeds, sea otters, and polar bears still retain their fur, but only because they maintain a semiterrestrial existence, spending time out of the water, where fur can be useful.

- Evolution often works in this way, creating the best compromise. Pinnipeds are neither perfectly adapted for land or water. They must settle for the middle of the evolutionary path. But the cetaceans adapted to a totally aquatic existence, so fur was not the answer.

- Therefore, the archeocetes, over evolutionary time, lost their fur. They met the challenges of diving, initially part time but eventually full time, into the cold ocean through the buildup of layers of subcutaneous fat to create the tissue blubber.

- Blubber is a fat layer that lies just beneath the skin of almost any marine mammal. Because it is rich in lipids, it can also secondarily act as an energy repository. Blubber is an amazing insulating material. Different species of marine mammal have varying thicknesses of blubber.

- Blubber is a common adaptation in almost all marine mammals, and it's also the final piece of the puzzle for the Antarctic-based penguins. It is blubber that allows penguins to dive for so long without succumbing to the temperature of the water.

TRY THIS AT HOME!

If you're not convinced about the efficacy of blubber, try this experiment:

Fill a bucket with ice and water and see how long you can keep your hand in it comfortably. Then, create a blubber mitt by coating the inside of a plastic quart bag with margarine (as a fat that represents the blubber) and then put a second bag inside the first bag. Now place your hand in that second bag and stick your mittened hand into the ice-cold water. You'll find that you can keep your hand comfortably in the water for much longer—because you now have a layer of insulating fat around your hand.

- The marine mammal blubber layer is not metabolically static; lipids are constantly being mobilized and replenished. In fact, for any one individual, blubber can vary in its density within a year, depending on an animal's migration and as a function of the temperature of the water in which they are swimming.

- Surprisingly, blubber might be too good at insulating the body. In pretty much every marine mammal species studied, we have discovered more mechanisms to lose heat, rather than gain it. Having too much heat buildup in the body is a problem because there are a number of essential life processes that can only work within a very narrow band of temperature. That is why humans use body temperature as a diagnostic of health and why temperature regulation is so important to our health.

Thermoregulation

- We can use whales as an example to show 2 ways that marine mammals can dump excessive, harmful heat. The first set of processes can be gathered collectively as physiological.

- Cetaceans have evolved a way to bathe vital organs that must remain constant in temperature in a network of blood vessels that deliver cooling blood. These vessels belong to a network referred to as the rete mirabile that also pass very closely to the surface of the animal in areas where the blubber coat is thin.

- This is directly analogous to the role a radiator plays in a car engine, where water is cooled and pumped through the warm motor. Because water has a high heat capacity, it can retain significant amounts of energy without increasing in temperature, so it takes the heat of the engine away back to the radiator, where it meets cooling air and dumps the heat to the environment.

- In the case of the whale, the animal's metabolism is the engine. The coolant pipes are the blood vessels, and the coolant fluid is blood. Furthermore, marine mammals have structures that are functionally very similar to radiators.

- For example, the complex network of blood vessels in a structure called the corpus cavernosum maxillaris was discovered recently in the upper palate tissue of the Arctic-dwelling bowhead whale. This fascinating organ, with a muscular structure very similar to the mammalian penis, is believed to become engorged and erect with blood when the animal is overheating. As the animal feeds, the organ is cooled by the inrush of cooling seawater to the inside of the mouth.

- Fascinatingly, all types of these "radiators" in animals bear a similar design mechanism. First, they have flattened surfaces that maximize the interactive surface between blood vessel and

the environment. Second, they present warmed blood in a flow direction opposite to the direction of the cooling environmental water. This design is called countercurrent exchange flow, and it provides a much more efficient method to exchange heat than concurrent exchange, where the 2 flow in the same direction.

- Key to the use of the retia mirabilia is controlling their flow. A complex series of valves open and close them, increasing the flow of warmed blood from the body to the surface during times of exertion and slowing the return of cooled blood when the body core temperature dips.

- This is very similar to processes in humans and likely is governed through a similar thermostat-like regulation through the form of a negative feedback loop, which works by being hindered by the effect it produces. For example, if an animal is hot, then the valves of the retia mirabilia are opened, and warm blood is freely exchanged with various cooling surfaces. This in turn cools down the animal, which then closes the valves to stop the cooling.

Marine mammals have about 10 times more fat in their milk than do humans. But even by feeding on the unusually fat-rich milk of the mother, it can still take up to a year or more for young mammals to develop adequate blubber tissue.

- In addition to physiological methods that facilitate thermoregulation, there is a second set of methods that can be loosely termed as behavioral. For example, semiamphibious marine mammals can return to the water to cool down.

- Seals are often seen basking in the Sun, either on land or in the water, with one flipper raised. By raising its flipper to the air and spreading it wide to expose the webbing, the seal is exposing a radiator surface that can dump heat to wind currents—even though it looks like the seal is doing the opposite and absorbing the warmth of the Sun.

- Pinnipeds have also been seen eating ice, and while the main purpose of this is likely to access a source of water, the cold ice would cool the buccal cavity that we know is heavily vascularized and is therefore capable of carrying warm blood.

- In the same way, a gray whale or bowhead might open its mouth during a migration not to feed, but simply to cool down from the exercise of swimming. In fact, migration itself is likely, in part, a response to thermoregulatory needs.

- The ocean varies in temperature, with polar waters perhaps 20° Celsius cooler than the tropics. Oceanic productivity is in part tied to that gradient, with polar waters being much more productive, and therefore more capable of sustaining food, than the tropics.

- If colder, higher-latitude waters provide more food, why not stay in those areas year-round? The answer seems to lie in the fact that young, smaller animals cannot thermoregulate at such low temperatures. This is probably because of 2 reasons. First, they initially lack the thick blubber tissues of their parents. The second reason has to do with a foundational principle within biology that has a dramatic effect on design: the ratio of surface area to volume.

- As an organism grows, the surface-area-to-volume ratio decreases. The surface of the organism controls what goes in and out, what is needed for metabolic processes, and what is exported as a result of that process, including by-products such as heat. In other words, the greater the surface area, the more efficient the transport of those products out of the organism, including heat.

- When an organism grows, its potential to produce heat increases, but ways to lose that heat through surface area do not increase as much proportionally. This means that large versions of warm-blooded organisms lose less heat per unit volume than their younger, smaller counterparts.

> Some scientists think that whales grow to such sizes—the blue whale, for example, at 30 meters plus—as a way to conserve heat. Through the mere act of being small, a smaller organism comparatively loses more heat than a larger one.

- Anything that increases surface area, including appendages that stick out and extraneous folds in the skin, are generally avoided in body design.

- The combination of having higher surface-area-to-volume ratios and less blubber tissue means that the small, young animals of a species are at a clear thermoregulatory disadvantage. They simply cannot tolerate a colder—albeit more productive, and therefore more desirable—ocean.

- This is where we believe the phenomenon of marine mammal migration derives. Adults give birth in the warmer waters of the lower latitudes. However, with respect to productivity, these

waters are relatively sterile. And that sterility means that the mammals cannot sustain their stay energetically, so they must migrate—when the calf or pup is thermally ready—to the colder, more productive higher latitudes. At the higher latitudes, they gorge on their food, readying themselves for an environmentally imposed fast on their return to low latitudes for the next birthing.

LECTURE SUPPLEMENTS

Readings

Castellini and Mellish, eds., *Marine Mammal Physiology*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Reynolds III and Rommel, eds., *Biology of Marine Mammals*.

Questions to Consider

1. In this lecture, you learn about how surface-area-to-volume ratio decreases with size of the organism. This might suggest that animals that live in colder climes should be slightly larger than their warmer-clime counterparts. Research the 2 species of elephant seal and the 3 species of right whale to see if this hypothesis is supported.

2. In some cases, adaptations to a cold environment may be insufficient to the task, in which case a marine mammal may choose to migrate to warmer climes. In some cases, these migrations may be quite temporary. Using the Internet as a research tool, review the behavior of the Antarctic killer whale: How does it respond to the cold temperatures of the Southern Ocean?

16

MAMMALIAN SWIMMING AND BUOYANCY

Marine mammals move in 3 dimensions, in the *x*, *y*, and *z* plane—corresponding to length, width, and depth. This lecture will focus on 2 issues that arise from living in a watery, 3-dimensional environment: how an organism may control its position in the *z* plane, or depth in the water column; and how the increased viscosity of water affects an animal's ability to move in that medium.

Achieving Buoyancy in Water

- Archimedes's principle states that an immersed object would receive an upthrust equivalent to the weight of the water it had displaced. We can apply this general principle to examine whether an object should float.

- If the density of an object is greater than seawater, then it will sink to a point where its weight equals the weight of the water it is displacing, at which we would say the object is neutrally buoyant. If its density is less than the surrounding water, the object will float, and we would say that it's positively buoyant. A negatively buoyant object is one whose mass exceeds the volume of water it is displacing.

- Most humans are naturally buoyant and will tend to float. However, we can change our buoyancy by changing our volume. The easiest way to do this is through the act of exhalation and inhalation. When we inhale while floating in the water, our lungs expand, and therefore we displace more volume. This, in turn, provides more upthrust, so we rise in the water column. But if we exhale, our lung volume decreases, so we sink slightly. The amount of air in an animal's lungs will affect its buoyancy.

- The problems and challenges that humans in water face are analogous to those that marine mammals deal with every day. Consider the case of scuba divers, who pay a lot of attention to their buoyancy. This is mostly because we don't want to expend energy in keeping our body at a certain height (or depth) in the water column. So, divers deliberately make themselves negatively buoyant to overcome the buoyancy of their equipment and then use a buoyancy compensator (BC) to increase their buoyancy to a neutral point, as needed.

- A buoyancy compensator is essentially a life jacket that can be partially inflated underwater. Divers simply fill the jacket with air from their tank until the overall amount of water displaced by the jacket achieves the required upthrust to counter the negative buoyancy of the diver. However, if the diver dives deeper, pressure will cause the jacket to collapse a little, so more air is needed to achieve the same neutral buoyancy.

- If the diver ascends, ambient pressure decreases and the air inside the jacket occupies an even greater volume, so the buoyancy is increased. If they are not careful, this can lead to a runaway effect where the BC provides greater and greater buoyancy with lessening pressure, leading to an uncontrolled ascent, which can be medically very dangerous. Divers are taught, as they ascend, to purge air from the BC so that the upthrust provided is kept right on the threshold of providing just enough, but not too quick, of an ascent.

Marine Mammal Buoyancy

- How do marine mammals invade the vertical dimension of water? Do they have the natural equivalent of a BC? Unfortunately, we don't know, although we do have some theories, and there have been some brilliantly designed experiments to investigate the problem.

- Part of the problem lies in knowing how much a marine mammal weighs. While possible for some of the smaller specimens of seal and dolphin, it is nearly impossible to evaluate the weight of a large whale with the degree of accuracy required to estimate buoyancy. And other than the lungs, there does not seem to be any specific anatomical structure associated with the act of being buoyant.

- We have measured the density of various tissues in a marine mammal. In the whales, for example, especially those species that are more polar adapted, a thick blubber jacket will aid in the buoyancy of the animal because lipids float. The thicker the blubber layer, the more buoyant the animal will be.

- Perhaps the best example of this are the right whales, which float when dead—because of a blubber layer that is upward of 30 centimeters thick. The fact that a right whale is buoyant means that it has to expend significant energy to dive. That effort would decrease the deeper the animal gets as the ambient pressure of the water crushes in on the body and causes it to displace less volume. But the start of the dive would be nonetheless costly. This helps us consider the problem of trade-offs in natural selection.

- The trait of having a thick blubber coat aids the right whale in reaching higher-latitude waters that are presumably more productive, so that is what an evolutionary biologist might call a positive trait. However, being well adapted to the cold means that the animal is very buoyant and therefore perhaps must spend more time at the surface. That could be a negative trait in terms of accessibility to food.

- Which wins out? To answer this question, an evolutionary biologist needs to consider all the costs and benefits of a particular trait. If the benefits outweigh the costs, then that trait is selected for. In this specific case, the prey of the right whale, mostly copepods, can be found at the surface, so the animal does not necessarily need to dive deep that often.

The right whale got its strange name from whalers because it was the right whale to kill. There are several meanings here:

- The animal was so buoyant that when killed, it would float. So, in hunting this species, the whalers did not risk killing the animal but then losing it before they could tie up to it.

- The blubber, once flensed from the animal, produced a high yield of whale oil, and therefore the whalers were more likely to make a profit.
- Because of their slow speed, they were easy to catch.

◇ Other whale tissues have unusual amounts of lipid in them. Whale bone, for example, is much more brittle and lighter than one would expect for the size of the organism it supports. Whales, as a fully aquatic species, do not have to support their full weight, so the skeleton does not have to be as strong. The bone is very porous, and each pore is filled with a droplet of oil. The overall effect of this is to reduce the density of the bone. This, in turn, makes the bone more buoyant.

- Blubber life jackets and light, brittle bones aid in buoyancy. But do marine mammals have built-in mechanisms that can dynamically alter buoyancy in a way that facilitates diving? Being able to dynamically change buoyancy in the same way a buoyancy compensator works for a human would help the animal minimize energy expenditure during diving, swimming at depth, and ascent.

- One possibility might be, as in humans, to control the amount of air in the lungs before a dive. By taking a breath before an animal dives, it has an expanded thoracic cavity that would cause more displacement, and it would be full of air, which of course would be buoyant. But this would increase the effort with which it would need to dive, and it would mean that the animal would have more respiratory gases on board that could complicate deep dives.

Whale skeleton articulators—for example, at the Smithsonian Institution—have known that there is oil in whale bones for many years. When they first collect the skeleton of a whale, they must find a way to dry it, to leach the oil out of the bones. Otherwise, the stench of the oil that leaks out from the skeleton over the years that it is on display to the public can be quite overwhelming!

- Correspondingly, the animal could deliberately exhale and therefore be negatively buoyant, but wouldn't that mean that the animal was diving with less oxygen, which it needs for its metabolism? The answer seems to be that marine mammals can either inhale or exhale before diving, but the deeper, longer dives performed by certain species are more typically associated with an exhaling action.

- Another possibility might be particular kinds of diving behavior. The humpback whale is famous for lifting its tail when it dives, a behavior called fluking. It doesn't do this all the time, but will almost always do so when diving deep. When the animal is doing this, it is performing the human equivalent of a duck dive—a behavior that humans use to reach the bottom quickly and overcome buoyancy issues.

- New technology is helping us to better understand the role of buoyancy in diving behavior. A new tagging technology, known as DTAG, has allowed us to follow animals fairly precisely as they dive. Importantly, DTAG are loaded with 3 accelerometers, one for each of the *x*, *y*, and *z* plane. So, we can follow the animal as it rolls, pitches, and yaws.

- In fact, the accelerometers are so sensitive that they can detect fluke strokes, which allows us to calculate stroke rate, and if we know the area of the flukes or tail, we can calculate thrust. If we know those 2 things, during an ascent or descent we can estimate how fast an animal should be going and compare that to how fast it really is going—the difference between the 2 must be due to either negative or positive buoyancy.

- DTAGs have shown us that marine mammal dives are far from linear.

The Viscosity of Water

- Perhaps the major challenge that a marine mammal has to face with regard to swimming is the viscosity of water, which is much higher than that of air. Any object moving through a fluid medium experiences drag—even humans, although we are so used to it at normal speeds that we don't really notice the drag of air.

- Drag also depends on the surface area of the body that is in contact with the fluid. This is why most marine mammals have relative simple body shapes with few folds and no more appendages than necessary. As a rule, any appendage, such as a propulsive surface, is relatively stubby and streamlined. Earflaps are reduced or nonexistent. Genitalia are internalized; fur is minimized, and so on.

- Finally, drag depends on the shape of the swimmer, an aspect that can be characterized in a constant known as the drag coefficient. The same elongated, teardrop, fusiform shape is found in almost every marine mammal that is highly dependent on swimming.

- Within the general fusiform shape there is variation, just as there is variation in the sustained and maximum speeds of different species. We can predict speed capacity through a mathematical expression known as the fineness ratio, which is the ratio between the body length and the maximum body diameter. Interestingly, the optimum shape that minimizes drag has a fineness ratio of around 4.5, and most marine mammals mimic that number.

- Actual swimming styles vary between marine mammal species. Phocids, for example, undulate their back and hind limbs in a lateral, or side-to-side, motion. In this motion, the hind limbs act like a scuba diver's fins, flicking back and forth, but thrust is also generated by the side-to-side motion of the posterior portion of the body.

◇ Otariid locomotion comes principally from thrust generated by the front flippers. This makes these animals unusually maneuverable; otariids can often be seen quite comfortably playing in breaking waves, their strong swimming style easily capable of overcoming the turbulence of crashing waves.

◇ Cetacean thrust is generated by dorsoventral oscillation of the flukes, so thrust is generated on both the up and the down stroke. It is also thought that even the compression of the blubber itself, and its desire to return to its normal shape, will aid in the stroke rate.

◇ As a rule, large cetaceans stroke at a lower rate and are slower than smaller cetaceans. This is mostly because large cetaceans do not need to swim as fast to catch the prey that they seek. And while they can certainly sprint, most larger cetaceans migrate over vast distances and therefore are more designed for stamina.

◇ To minimize wave-induced drag, marine mammals should stay at depth, which means that visits to the surface must be brief. But, of course, marine mammals are tied to the surface because they depend on snorkeled air, so they must surface.

◇ Cetaceans seem to follow this rule, surfacing 4 to 5 times before taking a longer dive, each time taking a breath. Behaviorally, this is called a surfacing sequence. During this time, they are busy exchanging the "used" air in their body with the fresh air of the environment. Then, when the animal is ready, it quickly dives and will stay down for an extended time that depends on the task at hand and the species involved.

◇ At high speeds, other behavioral responses can be used to reduce drag, including the act of porpoising. Various species of pinniped and small cetaceans do this; it is not restricted to the porpoises. Porpoising is the act whereby, during fast travel, an animal

arcs completely out of the water, inhaling as it does so to save having to return to the surface for a breath. While the animal is in the air, it is no longer suffering the effects of drag induced by the water. It is still experiencing drag from the air, but this is negligible compared to that experienced in the water.

LECTURE SUPPLEMENTS

Readings

Berta, Sumich, and Kovacs, *Marine Mammals*.

Reynolds III and Rommel, eds., *Biology of Marine Mammals*.

Questions to Consider

1. The next time you can use a mask and snorkel, experiment with your buoyancy. Try floating on the surface facedown and experiment with your lung size by taking in deep breaths and then exhaling fully. What does your body do in response? From your findings, do you think that a whale typically exhales or inhales before it dives?

2. What physical differences would you expect in terms of buoyancy between manatees and beaked whales? (Hint: First research the habitat in which they dive.)

3. In fish, we saw a distinct difference in caudal fin shape as a function of the animal's lifestyle: Some were sprinters while others were long-distance migrators; still more swam very little and relied on high maneuverability to avoid predators. Do we see similar adaptations within the cetaceans? (Hint: Examine the shape of the flukes.)

17

ADAPTATIONS FOR DIVING DEEP IN THE OCEAN

Marine mammals have evolved adaptations that enable them to dive deep to pressures that would kill humans. In this lecture, you will explore those adaptations—both how they work under ordinary circumstances and why they might fail.

Breath Holding

- Most humans, with training, can probably hold their breath underwater between 1 and 2 minutes at the surface if floating perfectly still, but any kind of activity or diving to depth will reduce that amount. When you think about holding your breath, you most likely get the image of you sucking air into your lungs, which act as the oxygen tank to store your spare air.

- In fact, that is only partially true. There are 2 other places in your body where you can store oxygen: in your blood and in your muscles. In your blood, oxygen is for the most part bound to hemoglobin, an important protein found in your red blood cells. These cells act as oxygen carriers and will disassociate their oxygen when they reach areas that need it to perform cellular respiration, which is the act of burning macromolecules to release their chemical potential energy. You can also find dissolved oxygen in your muscle mass, where the energy resulting from cellular respiration will cause muscle movement—an important use for oxygen.

The world record for a human holding their breath underwater is an extraordinary 24 minutes, held by a professional free diver.

◇ There are differences in the way that a diving marine mammal achieves this unusual capacity for storing oxygen. First, the blood of marine mammals has a second carrier protein called myoglobin, which has a higher affinity for oxygen than hemoglobin. This means that per unit volume, marine mammal blood can carry much more oxygen than human blood. Humans also have myoglobin, but it's typically only found after some form of muscle injury.

◇ Second, marine mammals downplay the importance of lungs as a gas storage site. This is probably because any air-filled space in a diving mammal is going to create serious complications the deeper the animal dives. It could also be an annoying source of buoyancy. So, as a rule, a marine mammal minimizes the lung space when at depth.

◇ In fact, pressure can often cause the lungs to collapse. This sounds disastrous, but it is actually an important adaptation and is quite reversible. Some marine mammals even have articulated rib cages that help the collapsing process.

◇ Lungs are still important to a marine mammal, but only at the surface. When the animal is at the surface, it must quickly and efficiently dump as much carbon dioxide as possible that has accumulated in the previous dive, and it must take up as much oxygen as possible and quickly shunt it to the blood and onto the muscle mass.

◇ During apnea, the physiology of a diving mammal is designed to save energy so that every molecule of oxygen is used in the most effective way. For example, marine mammals are capable of shunting their blood away from nonessential metabolic activities during a dive, sending the oxygen only to places where it is needed.

- It does this through a network of blood vessels referred to as the rete mirabile, a highly branched network of arteries and veins with a series of valves or sphincters throughout that can be open and closed, thus isolating physiological systems that don't immediately need oxygen and shunting blood to other areas of higher priority, such as the brain. The act of closing and opening these valves to various capillary beds is known as vasoconstriction and vasodilation, respectively.

THE CHALLENGES OF DIVING

The challenges of diving can be separated into 2 distinct categories.

1. As mammals returning to the aquatic realm from the terrestrial environment, marine mammals do not possess gills, which allow fish to extract oxygen at the low partial pressure at which it is available in water. But marine mammals have lungs, and lungs can't do that. Instead, marine mammals must undergo periods of apnea and rely on stores of air taken at the surface.
2. To hunt for their food, marine mammals must dive deep, often for extensive periods of time. The deeper the animal goes, the greater the ambient pressure. Among other issues, one potential consequence of this is decompression sickness, or the bends.

There is an extraordinary variability within the marine mammal group in terms of diving ability. Dive durations are also highly variable, ranging from minutes in the dolphins to a maximum record of an astonishing 2 hours plus in Cuvier's beaked whale.

Reducing Heart Rate

- The ability of marine mammals to reduce their heart rate at depth is called bradycardia. Marine mammal hearts are very similar to human hearts. They have 4 chambers and the same excitatory systems. In fact, a cetacean EKG looks very similar to a human EKG.

- The act of vasoconstriction and heart rate changes are all part of what is now more generically called the diving response, formerly called the diving reflex. A number of species are capable of a diving response, including diving birds—particularly penguins—and potentially humans up to the age of 6 months. After that point, our physiological behavior becomes too entrenched.

- One of the products of cellular respiration is carbon dioxide. Enzymes in the red blood cell cause the carbon dioxide to combine with water to form a hydrogen ion and a bicarbonate ion. As a result, the blood starts to become more acidic, a condition known as acidosis. This is actually a good thing, because it is high levels of carbon dioxide that involuntarily stimulate us to take our next breath—not our dwindling oxygen supply.

- This is why hyperventilation before breath holding is such a bad idea. The act of hyperventilation causes you to flush out the residual volume of carbon dioxide in your system. So, the respiratory system is "reset" at too low a level, and your system can be fooled into thinking that it can tolerate much lower levels of oxygen because your carbon dioxide levels aren't calibrated correctly. In reality, it can't, so you pass out from lack of oxygen.

- If a marine mammal's dive is long enough, eventually oxygen supplies will dwindle to the point that aerobic cellular respiration can no longer occur. Aerobic cellular respiration is the normal physiological state for mammals, one where oxygen is used to burn macromolecules to release their energy.

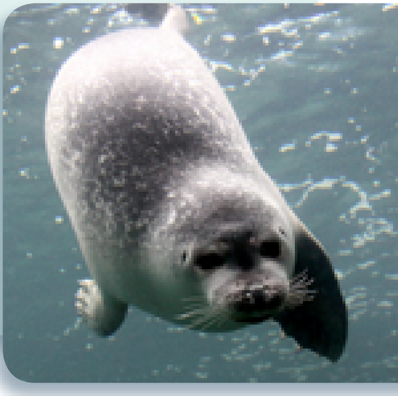
- However, in the absence of oxygen, cells may, for a limited time, perform anaerobic respiration. This is a slightly different metabolic pathway, not as effective or efficient, whereby some energy can still be yielded from the breakdown of a macromolecule. And there is a cost to this pathway: Instead of producing carbon dioxide, the body produces lactic acid.

- Excess lactic acid in one's bloodstream leads to acidosis, which is a reflection of a pH reduction in the blood. The buildup of lactic acid helps stimulate the need to breathe. However, it also makes both hemoglobin and myoglobin more willing to give up any oxygen they may have to the cells that need it.

- It is the buildup of lactic acid that causes the sensation of muscle fatigue. The only solution to this is to rest, a process whereby the lactic acid is broken down correctly, releasing the carbon as carbon dioxide. During this time, the body is said to be in oxygen debt. The body can only perform anaerobically for short periods of time before exhausting itself. It then needs to pay for the costs of running anaerobically.

In marine mammals, there appear to be 2 types of dive strategy: routine and extended. Routine dives comprise the majority of all diving behavior, and it is thought for the most part that routine dives are conducted within an aerobic regime.

However, once in a while, a marine mammal may need to dive deeper, or for longer, in which case it risks the possibility of shifting to anaerobic respiration. The threshold of switchover is known as the aerobic dive limit (ADL). Species that as a habit dive deeper or longer than others seem to be adapted to have higher ADLs. In fact, in general, marine mammals appear much more tolerant than humans to lactic acid.



Diving Under Pressure

◇ To a human diver, dealing with gases under pressure is a serious issue. First, both oxygen and nitrogen, the 2 gases most abundant in air, are toxic at higher pressures. At around 30 meters in depth, nitrogen toxicity can cause a phenomenon known as nitrogen narcosis, a condition that divers commonly refer to as the narcs. Beyond 50 meters or so, oxygen itself becomes toxic. The symptoms of such toxicities are serious enough that they can cause hallucinations, impaired judgement, convulsions, uncontrolled fits, unconsciousness, and death.

◇ Humans solve this issue by using a different mix of air in their scuba tanks that reduces the amount of nitrogen and oxygen through the partial substitution of helium. This is obviously not an option for a marine mammal, so how do they avoid nitrogen and oxygen toxicity? The answer is to minimize the amount of free-standing gas in the lungs at depth, and this is done by the mechanism known as lung collapse.

◇ As a marine mammal dives deeper, greater and greater pressure is exerted on the thoracic cavity, forcing the rib cage to collapse onto the lungs and thus also compressing them. However, the respiratory passages in the lungs are protected by cartilage in such a way that the alveoli, the blind sacs that represent the ultimate respiratory surface, collapse first. The bronchioles leading to the alveoli collapse second, and then the bronchi that lead to the bronchioles collapse last.

◇ In this way, very little air, or possibly none, is trapped in the lungs. It all gets pushed into tracheal spaces that are lined heavily with cartilage. It turns out that cartilage is impervious to gas absorption, so the little gas that is shunted to this area remains in the trachea and is not absorbed into the body, no matter how deep the animal dives.

- The act of collapse renders lungs useless as a source of respiratory gases during a dive, but marine mammals tend to hold their breath in their blood and muscle mass, so they don't need the lungs to perform that function.

- All other air spaces in the marine mammal are reduced or absent compared to humans; marine mammals don't have facial sinuses, and air spaces in the middle ear are further protected by compressible spongy tissue. This minimizes the effects of gases under pressure while at depth.

- The final problem that gases under pressure can cause is nitrogen decompression sickness, also known as DCS—or, its more common moniker, the bends.

- When a human dives with a regular tank of air, the gases the diver is breathing are immediately subjected to pressure as the dive becomes deeper and deeper. Nitrogen, being a metabolically inert gas, dissolves under pressure into our tissues. Depending on how long we stay at depth and under pressure, our tissues may become saturated with nitrogen, although any additional pressure caused by moving deeper will cause the tissues to absorb even more in this way.

- While we remain at depth, as long as we don't have to worry about nitrogen toxicity, the supersaturation of nitrogen in our tissues is not a problem. This is because nitrogen is otherwise metabolically inert. However, if we ascend too quickly, the lessening pressure will cause nitrogen to be released from our tissue too quickly in the form of bubbles that begin to expand as the pressure decreases even further. The expansion of these bubbles tears the tissues within which they were contained, causing lesions and hemorrhaging.

- In one of the worst scenarios, nitrogen bubbles in the bloodstream join with other bubbles to make even larger bubbles, and those bubbles can expand large enough to occlude blood vessels, particularly at skeletal joints, where there can be a natural narrowing of the vessel to allow the joint to flex. Occlusion means the cessation of blood flow in that particular part of our circulation system, which can be incredibly painful. The only temporary solution is to bend your body in the hope of relief, but this does not solve the problem. The result, if not treated, is death.

- In the mildest cases of the bends, we can reexpose the diver to the pressures experienced during the dive by placing the diver inside a dry hyperbaric chamber and then slowly, over a course of hours, bringing the diver back to atmospheric ambient pressure, allowing enough time for the nitrogen to off-gas naturally through gaseous exchange within the lungs. Surgery may still be required to fixed the damage caused by the original DCS event.

- But the best cure for the bends is prevention. In reality, we limit our time and our depth to minimize nitrogen saturation, and we leave enough time at the end of the dive to allow off-gassing of nitrogen at a harmless rate. Within our ascent, we might even create decompression stops, periods of time spent at certain shallower depths that are there specifically to help with off-gassing. Most divers carry dive computers that help them plan their dive in this way.

- How do marine mammals avoid the bends? For the longest time, there was a rote answer to this question: Marine mammals cannot get the bends. But researchers have now demonstrated that deep-diving whales can develop decompression sickness, especially if the animal dives repetitively in a series of shallower dives that do not allow time for nitrogen to off-gas naturally, or for the lungs to collapse, which would otherwise shunt nitrogen to areas where it would be harmless.

- ◇ Furthermore, researchers now believe that certain species may be particularly sensitive to decompression sickness because of the lipid structure found in various bodies of fat around the animal. These lipids may have an unusual affinity for nitrogen and thus retain it for longer than other tissues.

- ◇ To avoid decompression sickness, then, marine mammals must somehow incorporate into their ascent behavior a decompression schedule, similar to what we see in human diving—only in the case of the marine mammal, it's perhaps instinctual.

LECTURE SUPPLEMENTS

Readings

Ponganis, *Diving Physiology of Marine Mammals and Seabirds*.

Reynolds III and Rommel, eds., *Biology of Marine Mammals*.

Questions to Consider

1. Using the Internet, research the phenomenon of the human diving response. What are the parallels and differences between that and the marine mammal diving reflex? Why do you think this physiological response is only found in younger humans?

2. What is a decompression table, and what is a dive computer—both commonly used by human scuba divers? Obviously, marine mammals do not use these tools, so how do they manage to dive safely?

3. The Bohr shift refers to a physiological response that eases transfer of oxygen from the blood to organs under conditions of acidosis. Research the Bohr shift in humans and then in marine mammals. How is it different? (Hint: Think about the position of the oxygen disassociation curve.)

18

THE IMPORTANCE OF SOUND TO OCEAN LIFE

This lecture will journey into the marine mammal world of sound. Because we humans are visual creatures, that world is almost incomprehensible to us. But given the amount of time marine mammals have had to evolve in the inky oceans, it makes sense that they rely on sound to gather information about the world around them. Instead of seeing pictures of their environment in the way that we do, they probably "hear" pictures—an alien concept that requires a shift in our frame of reference as we consider how marine mammals might sense their environment.

Sensory Modalities

- The 5 principal sensory modalities are sight, touch, smell, taste, and hearing. There are some other less traditional ones that we tend to think less about because as humans, we simply do not have those abilities—for example, sensitivity to magnetic or electrical fields, both of which are possible underwater.

- If a species has 60 million years of natural selection to play with, it makes sense that a species will tend to evolve sensitivity in the sensory modalities that are most efficient in the medium within which that species lives.

- Because air is mostly transparent to light, vision typically becomes the most important sensory modality for terrestrial animals, unless they live in areas where light is limited, such as underground or in a cave. Humans are primarily visual creatures; we depend on vision to interrogate both our physical and biological environment.

- Underwater, vision is very limited for 2 key reasons. First, with depth, water gradually absorbs frequencies of visible electromagnetic radiation differentially so that eventually all that is left is a monochromatic deep-blue light. If you go deep enough, into the aphotic zone, there is no light; organisms in this zone must either make their own light through bioluminescence or depend on other sensory modalities.

- Second, transmission of light can be scattered by particles in the water. The concentration of particles in the water, or the water's turbidity, is highly variable and can include particles of sediment washed out from the shore or even planktonic cells.

- The upshot of all this is that light propagation can be very limited. In coastal regions, visibility can be as low as 0 meters. Visibility does get better as you move offshore, where plankton densities

are lower and you are away from the influence of land runoff, but even then, it's still not that good. So, why bother evolving a system that prioritizes an unreliable sensory modality?

- That's not to say that marine mammals don't have vision. Certainly, those species that live a semiaquatic existence still need fairly good eyesight for the times they are on land. Also, vision can aid in object identification at close range. So, most marine mammals have reasonable vision, except those that live in regions that are highly turbid.

- Chemoreception is a sensory modality that includes olfaction, or sense of smell, and gustation, or sense of taste. Semiaquatic species certainly use olfaction, because during the time they spend on land, the nares are open and that sense can work.

- Underwater, however, the sense of smell is off-limits, because the nares are closed to prevent aspiration of water into the lungs. So, for fully aquatic species, the sense of smell is less important, although some researchers have hypothesized the ability of cetaceans to smell the inhalation of air during a surfacing sequence.

River dolphins, as a rule, do not have good vision because the river habitat is often so opaque with suspended mud and sediment.

- There is good evidence that pretty much every marine mammal we have been able to test to date is capable of the sense of taste, if only because captive animals often seem to develop taste preferences in their food. However, for any chemical cue to be used as a method of detection of a source, the propagation path has to be clean, the cue getting stronger as one approaches the target. In reality, the chaotic nature of local water currents and turbulence tends to disrupt that propagation path.

- The sense of touch is definitely used in marine mammals. Many species demonstrate that they have extremely sensitive skin, and many behaviors rely on the ability to touch. Many fighting behaviors rely on a sense of touch. However, touch is a short-range sensory system. For it to work, one has to be in touching distance, by which time other senses will probably already have informed the animal of the presence of the target.

In cetaceans, a calf will often stay close to its mother as they swim, and the mother will often gently bump into or brush a fin against the calf to confirm that it is still there.

Sound

- Aside from magnetic field sensing, about which we know very little, and electrical field sensing, which we are fairly sure does not occur in marine mammals, this leaves the sensory modality of sound on which natural selection can work.

- Sound travels extremely well in water—much better than it does on land. This is because sound is made of a mechanical wave that creates a series of compressions and rarefactions in the molecules of the medium. Being relatively noncompressible, water resists these compressions and therefore wants to return to its original state as quickly as possible. So, the energy of the wave is well preserved, with little energy lost over distance.

- In this way, the wave radiates out spherically from a point source until it is interrupted by a change in the density of the medium, such as the seawater-seafloor interface, seawater-sea surface interface, or even oceanographic fronts. Once constrained by a boundary, spreading is more analogous to that of a cylinder expanding in diameter. As the sound energy is spread over an ever-expanding wave front, the signal becomes weaker.

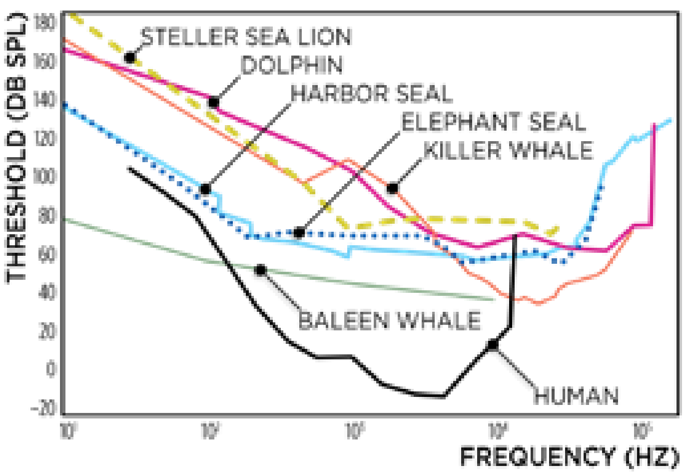
- Transmission can be highly efficient in water, depending on the frequency of the signal. Frequency is how fast the wave is oscillating back and forth across an imaginary line of zero displacement. We perceive the phenomenon of frequency as pitch, which is measured as cycles per second, or hertz.

- In water, high-frequency waves do not travel very far because they are quickly absorbed through frictional processes. However, under the right conditions, low-frequency sound can travel uninterrupted for hundreds, perhaps thousands, of kilometers.

◇ Different species have different sensitivities to sound. Frequencies too low for humans to hear—around 20 hertz or less—are termed infrasonic. Frequencies too high for humans to hear are deemed ultrasonic. Our hearing range decays over time, especially at high frequency.

◇ We can assess a species' hearing by graphing an audiogram, a diagram that plots frequency on the *x*-axis against threshold amplitude required to barely hear that sound. In this type of graph, mammals typically plot out as a U-curve—that is, there is an optimal frequency represented by the lowest part of the U that represents the frequency we are most sensitive to.

◇ For humans, that turns out to be between 3 and 5 kilohertz, not coincidentally around the same frequency as a human baby's cry. As we move outside of that peak frequency sensitivity, the sound has to be louder to be heard, until a point where no volume is sufficient for the sound to be heard.



- By comparison, marine mammal audiograms demonstrate amazing sensitivity to sound. This finding is not surprising given an animal that has evolved in an aquatic environment, where acoustic signaling is favored. Marine mammals typically hear well into the infrasonic and ultrasonic ranges of a human. In fact, they even produce signals in these ranges. Echolocation, for example, is typically centered around 30 kilohertz.

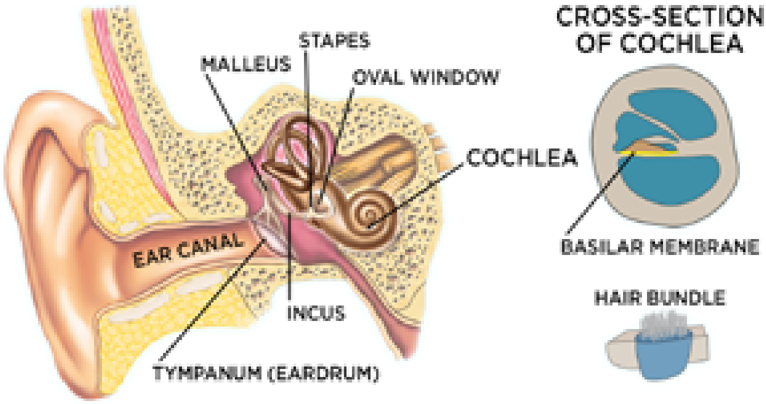
The blue whale produces a far-ranging moan so low in frequency that it is inaudible to humans.

Reception of Sound in the Ear

- Typical mammalian ears consist of an ear canal leading to a tympanum, or eardrum, that vibrates in the presence of an incoming sound wave. Attached to the tympanum, within the middle ear, are 3 bones that are unique to mammals: the malleus, incus, and stapes. These bones act to magnify the vibration of the tympanum. At the distal end, the stapes is connected via the oval window to the inner ear.

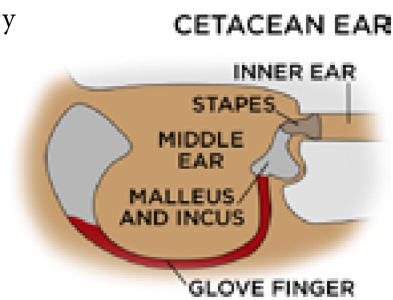
- The inner ear is a tube, known as the cochlea, divided longitudinally by the basilar membrane. Both sides of this membrane contain a jellylike substance that transmits the vibration throughout and across the basilar membrane.

- Finally, located on the membrane are a series of hairs that vibrate in the presence of an acoustic signal. Because of their specific position on the basilar membrane, each one of these hairs vibrates best at a particular frequency, triggering an auditory neuron to which it is attached. A multifrequency sound will stimulate a bunch of these hairs, each sending a nerve pulse down their respective neurons that the brain ends up perceiving as sound.



- Is there anything different about the marine mammal ear? Recent work on baleen whale ears has demonstrated that the design of the ear is specifically tuned to lower frequencies, especially infrasonics. So, not only do low-frequency waves travel far, but also large whales are very good at hearing them, even at low volumes. Other cetacean ears are also well adapted for frequencies relevant to their lifestyle; dolphin ears, for example, are designed, through the shape of their cochlea and basilar membrane, to hear ultrasonics, especially echolocation clicks, as high as 120 kilohertz.

- In addition, over evolutionary time, the cetacean tympanum has slowly morphed into an elongated structure known as the glove finger. Bizarrely, the outer ear canal is completely occluded with wax, so sound cannot travel in that way to the ear.



- ◇ We still do not understand how sound reaches the middle ear of a baleen whale, although we are beginning to think that elongated bodies of fat in the head of the animal might help channel the sound in that direction. In other words, the animal may receive sound through its forehead and rostrum.

Production of Sound

- ◇ As a rule, the stronger the amplitude of a sound wave, the further the propagation, on land or in water. We perceive amplitude as volume, which can be measured in decibels. Most cetacean-produced sounds are reasonably loud, presumably in an effort to maximize propagation, although our understanding of how these sounds are produced is relatively limited.
- ◇ The human voice comes from a pharynx associated with the trachea. Whales, however, do not possess a pharynx. Instead, they have a series of pharyngeal sacks, which may resonate at particular frequencies—in the same way that when you blow over an empty bottle, you can produce a note. The pitch of that note could therefore be changed by changing the volume of the sack, using muscles that squeeze around it. The air used to create the sound might come from that very air that was excluded from the lungs due to thoracic collapse during a dive.
- ◇ On the other hand, odontocetes possess a complex known as the monkey lips and dorsal bursa, a reference to the shape of the organ, and located just below the blowhole. Air passed through these tightly pressed structures causes a vibration that results in the various squeals and whistles, as well as the echolocation clicks that toothed whales can produce.

- In odontocetes, the produced sound is often modified by a structure known as the melon, a fatty-rich acoustic lens that sits on top of the rostrum. By altering muscle tensions around the melon, odontocetes can focus sounds into beams.

The field of marine mammals and sound is relatively new, and it is a challenging one in which to work, mostly because acoustics are difficult to model outside of experimental situations, and it is extremely difficult to create experimental situations using marine mammals unless they are held captive. So, most of what we know about marine mammals and sound starts with those animals that can be held captive. As a result, we know relatively little about how baleen whales might use and detect sound because a baleen whale has never been held in captivity long term.

Use of Sound

◇ In general, we can split marine mammals' use of sound into 3 categories: transmission of identity, behavioral synchronization, and environmental interrogation.

1. Perhaps the best example of sound being used to provide identity is found in orcas, or killer whales. Orca pods are organized along matrilineal lines—that is, the social system is organized around a matriarch. Each pod has a unique set of calls, known as a dialect, that is taught to the young. As they grow, the young retain these calls as part of their own vocal repertoire, and presumably—if it's a female—the orca passes the calls on to its young.

2. An example of the use of sound in behavioral coordination is that humpbacks and orcas use sound to coordinate hunting efforts. A humpback's trumpet or siren call is used to coordinate a group of animals as they engage in bubble-net feeding. In this behavior, timing is everything, and the call—among other purposes—seems to synchronize group behavior.

3. Sound can also be used to interrogate the environment. Using echolocation, odontocetes can resolve targets only centimeters across at distances of hundreds of meters. They can even determine the shape of the object, and if it is prey, how much fat it has, and likely the species.

LECTURE SUPPLEMENTS

Readings

Au, *The Sonar of Dolphins.*

Au and Hastings, *Principles of Marine Bioacoustics.*

Au, Popper, and Fay, eds., *Hearing by Whales and Dolphins.*

National Research Council, *Marine Mammal Populations and Ocean Noise.*

Richardson, Greene Jr., Malme, and Thomson, *Marine Mammals and Noise.*

Thomas, Moss, and Vater, eds., *Echolocation in Bats and Dolphins.*

Questions to Consider

1. Take a moment to think about the first 30 minutes of your waking day today. How much did you use vision to complete the tasks at hand? Could you have performed the same tasks with just the sense of hearing alone, blindfolded?
2. Using the Internet, investigate why a fin whale's 20-hertz pulse is so well adapted for long-distance propagation. How might natural selection have played a role in designing that sound?
3. Why is blue light the only light you see at depth?
4. Use the source-transmission-reception model to think about a sensory cue other than hearing.

19

FOOD AND FORAGING AMONG MARINE MAMMALS

In this lecture, you will learn about how marine mammals forage, the diet that they eat, and the adapted morphology that is used to obtain food. As heterotrophs, marine mammals rely on feeding to obtain the energy they need for the lifestyles they conduct. And because marine mammals are unusually large mammals, this can constitute the need for vast amounts of food.

What Marine Mammals Eat

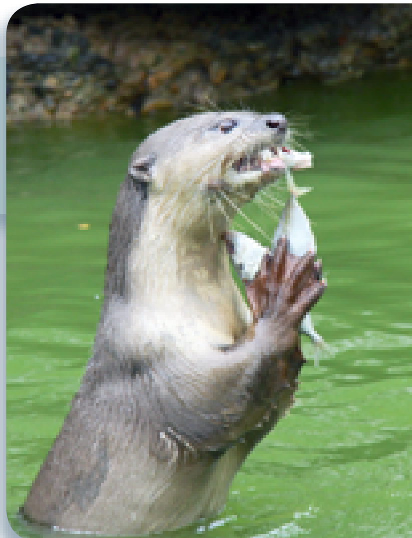
- What do marine mammals eat? We can answer this question in a broad sense, but getting down to the final details can be tricky for animals whose ingestion events typically occur below the surface. In general, marine mammals eat a variety of fish and invertebrates, including various species of squid, zooplankton, and other crustaceans. Their diet is rarely monotonous—that is, consisting of only one species—but variety in diet is highly species and region specific.

The humpback whale in the Gulf of Maine commonly focuses on 3 to 4 species, including herring, sand lance, squid, and krill. The northern right whale, in the same region, focuses on a few species of copepod, with only one of those species being taken in substantial numbers.

- We also see an ontogeny in diet choice. As mammals, young will nurse for a period of time before becoming independent from their mothers. Length of nursing is highly variable, lasting from a record few days in the hooded seal to potentially years in the sperm whale calf, which may receive milk for up to 2 years or more. Once the animal weans, it must start to hunt on its own, and early on it may lack the coordination for some of the more complex behaviors developed to capture the most elusive of prey.

◇ How do we know what an animal is feeding on? In a very few cases, we can witness a successful ingestion event. This is particularly true of semiterrestrial predators, such as polar bears feeding on various species of seal or a sea otter lying on its back using tools to crack open a bivalve. However, for marine mammals, more often than not, the ingestion event occurs below the surface. How, then, do we know what the animal is feeding on?

The sea otter's potential menu of choices is more than 100 species, and different individuals within the same population often express specific preferences.



◇ Sometimes we may not know for sure, but we can make a reasonable deduction. For example, if we see a group of whales repeatedly fluking in the same area, spending little time at the surface but constantly revisiting the same patch of water, one interpretation of that kind of behavior might be that they are feeding.

◇ We might even note that there are certain prey species co-occurring in the water with the "feeding" whales. Perhaps we see evidence of schooling fish. Perhaps we see that the water has turned a reddish color because of the presence of krill.

◇ In an even less direct association, maybe we see feeding seabirds around the area. If, for example, we see a flock of diving gannets clearly feeding on a school of prey and we see repeatedly diving whales in the same region, we might make the assumption that the whales are indeed feeding, perhaps on the same species on which the gannets are foraging.

- As unscientific as these techniques sound, they have all been used at one time or another to infer *that* a marine mammal is feeding. They are less useful as techniques in inferring *what* the animal is feeding on. For that, we have to see the actual ingestion event or find evidence of the prey in the consumer.

- Finding evidence of the prey in the consumer can be fairly invasive. In the past, it was common to analyze the contents of the gastrointestinal tract for evidence of undigested parts of prey—often those parts that resist digestion, such as bone, otoliths, squid beaks, or squid pens.

- This was a form of science that was inevitably linked to the whaling industry, which provided a plethora of carcasses to examine. And as heinous as the process of whaling was, in the early days, much of what we understood about whale diet came from these kinds of study. However, there are errors, or biases, in this approach. And there's an ethical point, too; the whale had to die for us to obtain these data.

- Since the cessation—for the most part—of whaling, we have found other, nonlethal ways to examine gut contents. In fecal analysis, we examine the animal's scat for those same identifiable hard parts of prey that remain undigested and have been voided out of the intestinal tract. This, however, can mean following an animal around for hours if we want to attribute the scat to a specific individual. We can also perform stomach lavage, which is a fancy phrase for the stomach pump, whereby we examine the regurgitate obtained from sticking a tube down the animal's esophagus.

- Scat analysis is more suited to larger animals in the wild, such as whales. Stomach lavage is fairly invasive and requires capturing the animal, but it can be done safely—with the correct training—on smaller pinnipeds in situ. However, both of these techniques still carry biases; the only thing we have gained is that the animal is still alive at the end of the day.

◇ With advances in technology, we are now able to use more sophisticated techniques. The food you consume, if absorbed and assimilated into your system, will eventually be deposited somewhere in your body, often at storage sites, such as subcutaneous tissue, or in other tissues layers that have high metabolic turnover, such as blood or skin.

◇ There are 2 techniques that can be considered tracer methods that can be used to identify the food once it has been deposited. The first, known as fatty acid analysis, looks at fat composition in a consumer. Fat is made up of a series of fatty acids that at a molecular level vary in their chain length, weight, and ratio of single- to double- to triple-bonded carbons.

◇ If one analyzes for enough of these fatty acids, one starts to see patterns of fatty acids attributable to certain species. In other words, a prey species would have a fatty acid signature unique to that species that would consist of a number of fatty acids of differing molecular weights in specific proportions to each other.

◇ If a consumer forages on only one species for its life, its fat tissues would take on a signature very similar to that of its prey, with a few modifications. If the consumer takes 2 species of prey, then its fat tissues would look like a combination of those 2 species of prey, weighted by the proportion of each species type in the diet.

◇ The more prey species a consumer takes, the more complex its fat signature would be, so in reality this technique does have limitations, and it requires a fairly sophisticated statistical analysis. That said, we have used the technique to look at diets in both pinnipeds and cetaceans with good success.

◇ Importantly, because we are looking at a tissue that accumulates information over time, we can use this kind of technique to look at a historical average of diet that would be a function of the turnover of that tissue. Fat tissues are notoriously stable

compared to most, so we can use this type of analysis, called quantitative fatty acid signature analysis (QFASA) to look at past diet in the order of months.

- In addition to fatty acid analysis, a second tracer technique is called stable isotope analysis, in which we look at a biopsy sample and determine the ratio of certain stable isotopes—usually carbon 13 and nitrogen 15—to their more common forms—in this case, carbon 12 and nitrogen 14. Those ratios can be indicative at least of the trophic level at which the consumer is feeding, and when one looks at the 2 measures simultaneously, they can even be used to infer species consumed. Similar to QFASA, stable isotope analysis examines food signals integrated over weeks to months, depending on the tissue investigated.

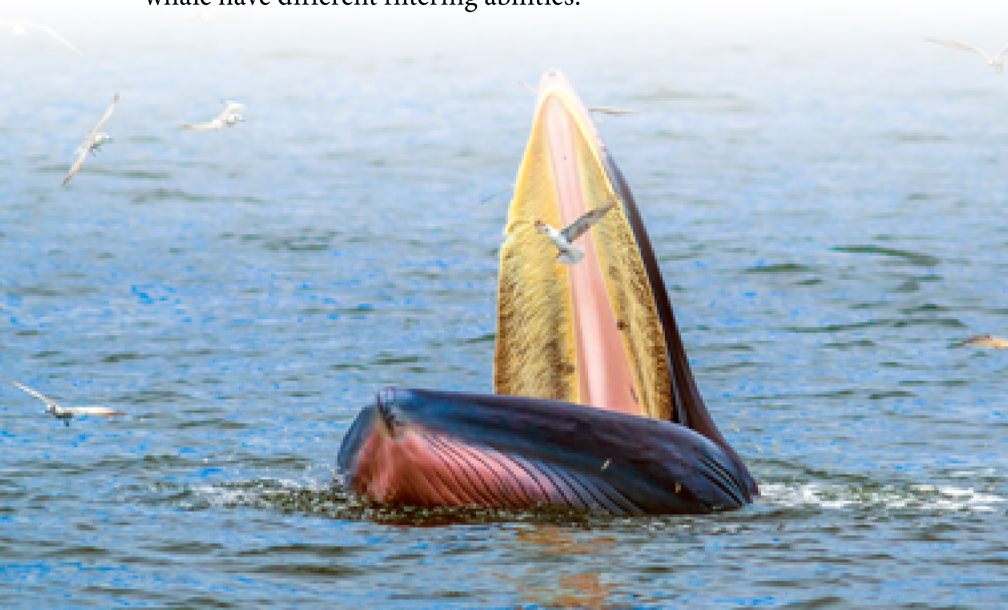
A polar bear will eat a ringed seal, which in turn eats arctic cod or herring. Those fish species eat zooplankton, such as krill or copepods, and those in turn eat phytoplankton. This is an example of a 5-step chain, or one that contains 5 trophic levels. Unless we in turn were to eat the polar bear, it would be difficult to add another level in there. And this is something that we find in general to be true of marine trophic dynamics: There are rarely more than 5 levels in any example.

Hardware Animals Use to Acquire Prey

◇ Thought to have developed from gum tissue, baleen is a keratinous material that is organized into a series of plates that hang from either side of the rostrum of baleen whales, or mysticetes. The plates are so designed that the edge facing the outside of the animal is fairly linear and unbroken. However, the edge facing into the mouth tends to fray into individual strands that then overlap each other, in effect creating a mesh on the inside of the mouth.

◇ It is this mesh that is responsible for filtering seawater for food organisms, whether that be microscopic prey or larger fish or squid. The mesh captures the organism, and the water is allowed to pass freely out of the mouth.

◇ In other words, the baleen whale carries a natural fishing net around on the inside of its mouth. The size of the holes in the net are a function of how finely the baleen frays and how many baleen plates there are per side of the jaw, both a function of which species we are examining. So, different species of baleen whale have different filtering abilities.



- Aside from baleen whales, the remaining marine mammals possess teeth. Tooth design tends to reflect the diet to which the species is adapted, so understanding the tooth morphology of a marine mammal is a way of finding clues to the animal's feeding lifestyle.

- Dolphins and sperm whales, for example, have conical teeth designed to grasp, although whether or not that is what the tooth ends up doing depends on the species.

- In the dolphins, the teeth appear to serve exactly that purpose. There is no chewing—simply a grasping of prey. If the animal wants to eat smaller amounts, it will rip the prey by shaking it back and forth violently while holding it in the teeth. Pinnipeds do this, too.

- In the sperm whale, however, the teeth may not serve that purpose. Sperm whale completely lack an erupted set of upper teeth and instead have sockets into which the lower set fits. The fact that whalers have found entire, intact squid in the stomachs of sperm whales implies that the whale might swallow them whole. A current working hypothesis is that sperm whales might use concussive clicks to stun their prey, which can then be slurped up. A co-hypothesis is that squid might be attracted to bioluminescent bacteria growing in the gum line of the sperm whale's jaw, perhaps remains of a previous squid meal.

- In the marine mammals, different teeth also suit different types of diet. Many Antarctic seals, for example, have sets of teeth that exhibit functional occlusion—that is, the teeth from the lower jaw fill the spaces left by the teeth in the upper jaw, and vice versa. Because the teeth are also multicuspate, this leaves gaps within the teeth through which water can flow. This is a filtering design, just like baleen.

- Nowhere is there a better example of this than in the crabeater seal, which needs to filter water to obtain krill. In a set of closed jaws, the teeth fit together extremely well, and the filtering mechanism that is formed represents a much more efficient method of prey acquisition than the alternative, which would be for the seal to chase down every krill individually.

- Lastly, some marine mammals possess very few teeth, no teeth, or teeth that are so bizarrely formed that they cannot act in the way that we typically expect teeth to act. Animals with few or no teeth likely use other ways to obtain food—for example, we believe that many of the beaked whales use suction to slurp up their prey.

Perhaps the strangest species of all beaked whales is the strap-toothed whale. In this species, only the males have teeth—just one pair that erupts out of the mouth and curves over the top jaw like a pair of tusks. This actually limits how far the whale can open its mouth. This might seem maladaptive, but perhaps the teeth are not used in their traditional role; perhaps they play a role in courtship or mating.

LECTURE SUPPLEMENTS

Readings

Castellini and Mellish, eds., *Marine Mammal Physiology*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Reynolds III and Rommel, eds., *Biology of Marine Mammals*.

Questions to Consider

1. Think about the meal you had today for dinner. Trace back each trophic step to the level of primary production. Estimate—using the 10% rule described in this and previous lectures—how much primary productivity was required to produce that meal.

2. Think about the ways in which humans are adapted, both morphologically and behaviorally, for the types of diet we consume.

3. Using the Internet, investigate cooperative feeding behavior in 2 examples: orcas and humpback whales.

4. How might feeding behavior be tied to the phenomenon of migration?

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MARINE MAMMAL INTERACTIONS WITH FISHERIES

Humans have been fishing for thousands of years, and for much of that time, our efforts were low and sustainable. However, with the birth of the Industrial Revolution, our abilities to fish exploded. Not only did vessels get bigger and more powerful, but our capacity to haul larger nets also increased. In the 20th century, plastics and nylon became much more common as materials from which to make lines and nets. These materials had a much greater half-life than anything that had come before and were also much stronger.

Tuna Fisheries

- Although negative marine mammal interactions had been occurring before, it was in the latter half of the 20^{th} century that many fishing-related issues came to a head. Animals would frequently run into, and get entangled in, nets and lines, the result often being their death.

- Technically, this type of mortality is referred to as bycatch, which is the capture and retention of any species in a net not targeted by a fishery. For as long as we have been fishing, bycatch has been an issue; however, the plight of marine mammal bycatch was brought to the public's attention by a very particular fishery: the eastern Pacific tuna fisheries of the late 1950s, 1960s, and 1970s.

- Dolphins were known to swim with tuna schools because they often sought the same prey. Because dolphins are much more observable at the surface than tuna, fishermen would often look for the dolphins as a way of finding the large tuna schools. Once found, the school would be surrounded by nets—known as purse seines—that could not discriminate between tuna and dolphin, so both were often killed.

- It was suspected that millions of dolphins were killed in this way without the public ever knowing the true cost of their store-bought tuna—a cost that in fact represents what we now suspect to be the largest marine mammal bycatch ever.

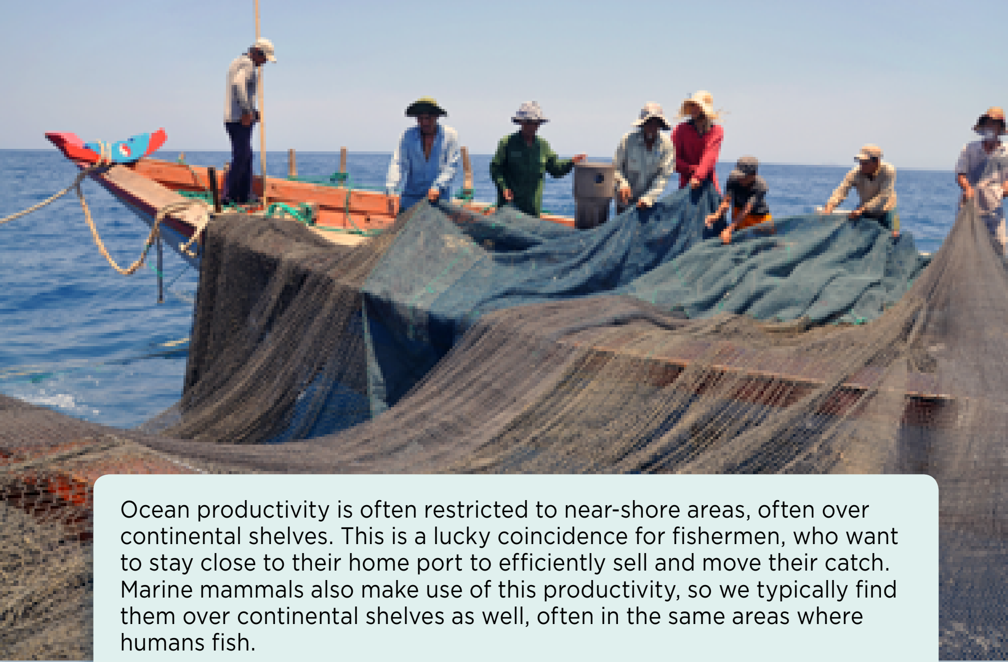
- But in the mid-1960s, this all changed. The media became aware of the issue, and together with the growth of the environmental movement, the public deemed dolphin bycatch unacceptable. Opinion was swayed by graphic, violent, and bloody images of dead dolphins lying on the decks of tuna boats.

◇ It was probably the tuna-dolphin issue, together with the appalling consequences of whaling, that inspired what has become perhaps one of the most important conservation laws in the history of the United States. In 1972, Congress passed the Marine Mammal Protection Act. We, as a society, are forbidden from harming marine mammals, or supporting any activity that might harm a marine mammal, irrespective of its endangered status.

◇ The tuna fishing industry was given 2 years to come up with new best practices and new technology that would reduce bycatch to "insignificant levels approaching zero." To their credit, perhaps because of the enormous legal pressure put on them, the industry did react appropriately, instituting new methods and technologies that reduced the annual mortality rate from half a million dolphins to around 20,000 individuals.

◇ This was a good result for U.S.-flagged fisheries, but global demand for tuna increased, so dolphin bycatch mortality increased again. The United States was powerless to change this directly, but in a smart move by legislators, the United States deemed that tuna imports could only come from international companies that agreed to adopt similar bycatch reduction strategies. This action was surprisingly effective, probably because at the time, the United States was a significant importer of tuna fish.

◇ This led to the idea of the dolphin-safe label found on store packaging today. While some still criticize the efficacy of such a label, it nonetheless highlights the importance and utility of attacking a sustainability issue from the market end of the problem; if one makes the market more selective, then producers must respond in kind. Today, in the United States, the only kind of tuna you can buy is dolphin-safe tuna. That said, the enforcement and observer efforts of so-called dolphin-safe tuna fleets are far from adequate.



Ocean productivity is often restricted to near-shore areas, often over continental shelves. This is a lucky coincidence for fishermen, who want to stay close to their home port to efficiently sell and move their catch. Marine mammals also make use of this productivity, so we typically find them over continental shelves as well, often in the same areas where humans fish.

Human fishing and marine mammal distributions often overlap not necessarily because they are targeting the same fish species, but because oceanographic and bathymetric processes lead to the productivity that draws both humans and marine mammals to the same spots.

Cetacean and Pinniped Bycatch

- Other toothed whales and pinnipeds can also be killed as bycatch. For example, in the northeastern United States, harbor porpoises seem particularly susceptible to gill net entanglements.

- Gill nets and purse seines work in a fundamentally different way. Purse seines seek to surround and entrap a school of fish. Slowly, as the net is hauled in, the pound within which the fish is entrapped becomes smaller and smaller, and the school of fish becomes more and more densely packed. Eventually, the fish are tightly enough grouped that they can be removed by dip net or a giant underwater vacuum tube into the hold of the fishing boat.

- In spite of the dolphin-tuna problem, purse seining is considered a fairly sustainable form of fishing that yields a high quality of fish, because it is alive up to the minute it is brought onboard the boat.

- Gill nets, on the other hand, are large panels of net often made from monofilament nylon. They can span kilometers in length and can be set anywhere in the water column. Unlike a purse seine, which is actively monitored by the people fishing it, a gill net is set and then left. The mesh size is designed to entangle fish by their gills. Unable to maintain the movement of oxygenating water over their gills, ensnared fish die and are retrieved by the fisherman perhaps days later.

- Gill nets can also catch small odontocetes, such as porpoise, as well as various pinniped species. These nets can be lethal, and they are particularly so for smaller marine mammals. Once entangled, they cannot rise to the surface for a breath, so they commonly drown.

Flying fish trapped in gill net

- Mitigating this kind of problem requires a very different kind of solution than the tuna-dolphin issue. In the case of a purse-seine system, one side of the net can be lowered and the animals can be driven over the net to freedom. Also, tuna fishermen can choose to try to not encircle a dolphin pod that they might be following in the hopes of finding tuna.

- In the case of gill net bycatch, the entanglement happens below the sea surface, unseen and unattended by the fishermen. The animal is dead by the time the fishermen return to haul the net. What is needed instead is a way of preventing the animal from hitting the net in the first place.

- The ways that this can be done can be divided into 2 general types of solution. In the first approach, we limit where and when fishermen operate to minimize the possibility of overlap between marine mammal and fishing net distribution. For example, if a species of dolphin is known to use a particular critical habitat for part of the year, then for that period, fishing should be banned in that area.

- Such strategies are known as time and area closures, and they have met with some success, although they are often unpopular with fishermen who visit those fishing grounds because they are productive areas and therefore represent a source of income that is now threatened because of federal intervention.

- Another possibility is to improve the detectability of the net so that an animal will detect its presence in time to avoid it. The evidence suggests that most marine mammals seem capable of detecting the net, but only at close range. Yet what we know of dolphin echolocation indicates that they should be capable of detecting a net at some distance.

◇ Perhaps when porpoises and dolphins hit a net, they do so because they are not expecting it to be there and are therefore not looking for it. Nets are designed, after all, to be cryptic—that's why they are so successful in catching fish.

◇ How, then, does one make a net more noticeable? Knowing as we do that fully aquatic marine mammals place great importance on the sensory modality of sound, perhaps there are ways to ensonify a net, to make it more acoustically obvious. A number of different ways were tried until researchers eventually developed an electronic beeper that one could hook onto the net.

◇ Relatively cheap to make, the beeper, or pinger, emits a high-frequency beep at regular intervals. They are waterproof, and the batteries that power them work for reasonable periods of time before they have to be replaced. All the fisherman has to do is to attach them at intervals along the net.

◇ It would be wrong to call these beepers alarms, because they do not serve to scare an animal away from the net. Rather, they draw the animal's attention to the fact that something is there—something that would encourage them to bring their full suite of senses to bear in order to investigate. In that sense, perhaps, they are better known as alerts.

◇ For the most part, pingers seem to be successful in reducing dolphin and porpoise bycatch. Importantly for the fishermen, they emit a frequency that is audible to an odontocete but outside the hearing range of a fish.

◇ Pingers, however, have created some problems for interactions with pinniped species. Given that the purpose of a pinger is to advertise the presence of a net, some seals have learned to use the sounds to localize where they might find a freshly caught meal of fish. Researchers refer to this as the dinner bell effect, and it is

an example of a larger problem known as depredation, whereby marine mammals sometimes take a fisherman's catch from his nets or lines.

- In an effort to prevent seals from using pingers as dinner bells, some researchers thought to turn the alert into an alarm—and so was born the acoustic harassment device (AHD). This gear emits sound so painfully loud that in theory, animals would not want to be near it. The more sophisticated AHDs cycle their emissions from quiet to loud, thus displacing animals away from the source over a reasonable period of time.

- Although they sound like a good idea, in reality AHDs have had mixed results. While we have significantly reduced the small cetacean bycatch problem, pinnipeds remain problematic.

Large Whale Entanglement

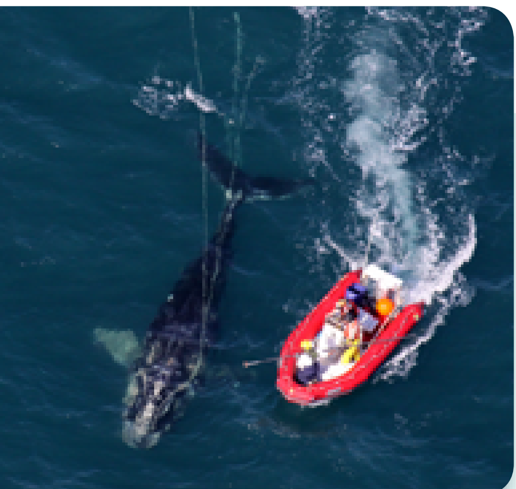
- Perhaps one of the most challenging bycatch situations is that of large whale entanglement, which became a significant problem in the mid- to late 1970s and again seemed to coincide with fishermen switching to nylon and plastic products that created much stronger lines and netting.

- As strong as whales are, when a large amount of nylon-enhanced mesh gets twisted up into a cable, it proves almost impossible to break. Any species can get entangled, although the species with more knobs and bumps, such as right whales and humpback whales, seem particularly susceptible.

- An important difference, however, when compared to small odontocete entanglements, is that large whales can survive being entangled for months, towing the gear around with them.

Sometimes the animal might break free on its own. It's only if the entanglement is particularly severe, impeding feeding or motion, or if the animal becomes fixed to the seafloor that the entanglement becomes serious and potentially lethal.

- ◇ In Canada in the late 1970s, humpback whales moved their feeding grounds from the offshore waters of Newfoundland into the inshore environment, where many Newfoundlanders fished for cod using gill nets and fishing traps, a type of gear similar to the purse seine, only fixed to the ground.
- ◇ It was almost inevitable that the world of whales and gear would collide, because both the whales and the cod that the fishermen were after stayed inshore to fish for capelin, a herring-like fish that schools in the millions.



The United States shares a remarkably similar story of large whale disentanglement with Canada, but with some important differences. Notably, although humpbacks and minke whales get entangled in the United States, of far more concern are North Atlantic right whale entanglements. Right whales are highly endangered, so great effort is placed into rescuing them. Also, unlike the Canadian situation, there is still a lot of fishing gear in the water in the United States, and fishing gear entanglement remains a significant source of mortality for several species of whale.

The act of entanglement must be extremely painful to the animal. One researcher has even argued that the act of whaling is, in fact, much less cruel because the animal's death is comparatively instantaneous.

And if we, as the general public, can be incensed enough about whaling to demand change, why aren't we just as fired up about the problems of marine mammal bycatch? The answer is likely that not many people know about it. When public awareness is high, as it was in the case of the dolphin-tuna conflict, governments are forced to act, resulting in change.

- The first few entanglements were disastrous for both whale and fisherman. The whale typically lost its life, and the fisherman lost his net—in those days, an expensive and uninsurable hit on the fisherman's income. No one seemed to know quite what to do.

- In desperation, one fisherman turned to a marine mammal research group at the local university to see if they could help with a whale he had found anchored in his gear. A researcher came out, and operating from a small inflatable vessel, armed with no more than a knife and a few grapnels, he freed the whale and saved the net at the same time—a win-win situation. That was the beginning of a large whale disentanglement effort in Canada, specifically for humpback and minke whales.

- But the disentanglement of whales was a Band-Aid solution. The goal needed to be to prevent the animal from hitting the net in the first place. Eventually, researchers designed a pinger that

any fisherman could build in his shed with a quick visit to the hardware and electronics stores. The evidence pointed toward pingers as being very successful in reducing bycatch.

◇ Then, in 1992, the federal government closed the cod fishery. All the nets came out of the water, and the problem of disentanglement was greatly reduced. We had, and still do have, the odd entangled whale, but not in cod-fishing gear and, these days, not typically inshore. With time, the whales appeared to have moved farther offshore, as have fishing practices.

LECTURE SUPPLEMENTS

Readings

Center for Coastal Studies, "Marine Animal Entanglement Response."

Johnson, *Entanglements*.

Krauss and Rolland, eds., *The Urban Whale*.

National Oceanic and Atmospheric Administration, "Marine Mammal and Sea Turtle Stranding and Disentanglement Program."

Questions to Consider

1. You have been charged with fixing the problem of right whale entanglement in fishing gear. Who would you bring to the table in that first meeting? What groups must be represented?

2. Research the histories of Dr. Jon Lien and Dr. Charles "Stormy" Mayo, 2 key figures in the large whale/fisheries entanglement problem in Canada and the United States, respectively. What are the common themes and differences?

3. If you were to design an acoustic whale alert, what would its key features include?

21

BREEDING AND REPRODUCTION IN A LARGE OCEAN

The nursing bond that exists between mammalian mother and calf creates an altricial bond that is unusual in the animal world. Most organisms adopt a precocial strategy: The offspring are relatively independent of their parents, there is minimal parental investment, and to compensate for the inevitable reduction in survivorship of the young, parents typically produce thousands and thousands of offspring. The altricial strategy is to produce few young and maximize parental investment to ensure their survival. Pregnancy results in a single pup or calf, in which there is then significant parental investment, typically by the mother. This lecture will focus on the reproductive and life history strategies of marine mammals—specifically pinnipeds and cetaceans.

Reproductive Systems

◇ From a biological perspective, the goal of life can be reduced to very simple terms: to pass down one's genetic material to future generations. The capacity of an organism to do this is referred to as its fitness. The sum total of an animal's behaviors, morphology, and physiology will be manipulated by natural selection to maximize fitness.

◇ An expanded definition of this might also include strategies and adaptations that help kin survive—by helping them, you also maximize the chance that genetic material common to you both will be passed on to the next generation, if not through your own offspring. This more expanded definition is referred to as inclusive fitness. Natural selection acts on an organism to ensure that inclusive fitness is maximized.

◇ Maximizing inclusive fitness is a very important concept specifically in considering life history, because it helps explain the variety of strategies animals adopt to ensure successful reproduction. To pass on their genetic legacy, marine mammals must meet the challenge of successful procreation in the marine or semiaquatic environment. However, there is rarely a one-size-fits-all solution. Instead, there are different strategies that are usually species specific that have been developed over evolutionary time through the process of natural selection.

◇ What drives natural selection to choose one strategy over another? One might say that the evaluative tool is inclusive fitness. Costs and benefits are weighed, and the strategy that results in the greatest gain in inclusive fitness will be selected for, because on average it will be those individuals that successfully reproduce.

- As a rule, because females produce relatively few eggs, a female's role in reproduction is limited by resources such as food, adequate territory, safety, and access to mates. Males, on the other hand, produce thousands upon thousands of gametes. All they need to do is to fertilize those eggs. Biologically, they need not have anything to do with raising the young; calves or pups do not have the same physiological dependence on the father as they do the mother. Therefore, male reproductive success is linked to their access to females.

- These 2 very different gender-based perspectives tend to naturally lend themselves to the creation of polygynous systems—one whereby one male will mate with many females. And indeed, as a general rule, that seems to be the case.

- Where pinniped and cetacean reproductive systems have been studied with relative rigor, males appear to try to mate with as many females as possible. However, there is an important caveat: Cetacean breeding is difficult to study because the animals are fully aquatic and we cannot follow them 24/7, so we know much more about mating systems in the pinnipeds.

Pinniped Mating

- One of the best-studied pinniped mating systems is that of the elephant seal, perhaps one of the most extreme forms of polygyny that has been found in the animal world. Elephant seals exhibit extreme sexual dimorphism; males and females have very different appearances.

Southern elephant seals (*Mirounga Leonina*)

- In the southern elephant seal, females weigh around 800 kilograms and are perhaps 2.75 meters long—huge for a seal. Impressively, the males weigh 3 or 4 times more than the females and measure almost twice as long.

- A seminal paper written in the 1960s helps us understand where this dimorphism comes from, demonstrating that in this case, the 2 driving factors appear to be the fact that food is located in the offshore environment, in the water, yet elephant seals are tied to the land for birthing, or parturition.

- In general, the fact that food is located offshore in a marine environment will tend to select for larger animals, because to survive the cold water, one must build up a significant mass of subcutaneous fat, or blubber, that can also act as a food reserve, allowing for periods of fasting while on land.

- Because females must remain on land to give birth, and because of all the sites available to haul out only a few are suitable, females tend to be naturally gregarious. They are much more tolerant of each other socially. Nursing females provide milk for a very specific length of time, usually around 3 weeks, at which time the mother cuts the bond with the pup and becomes sexually receptive. Once it has mated, it heads to sea.

- Male elephant seals, on the other hand, are quite antisocial. They fight other males for access to females in spectacular sumo-style fights. These bouts last minutes and are typically won by the larger male. Larger males will therefore tend to be reproductively successful, having greater access to mates and therefore maintaining the larger harems. Larger males tend to sire larger males, so the selection for larger and larger males is reinforced.

- However, successful copulation by the winning male, the one called a beachmaster, is only guaranteed if he can stop other males from mating with his consorts after he has. This means prolonged periods of guarding the harem after copulation to prevent the intrusion of other males.

- The animal's large size not only helps him win fights, but also helps him fast for longer on the beach, guarding the females. A hungry male has to return to sea, temporarily abandoning his harem to possible intrusions from other males. Again, large size in the male is selected for to help reinforce this ability.

- This is an example of a species that is tied to the land for the birthing process. Because females typically come into estrus just after weaning their pups, mating is generally tied to that time as well; the herd is together at that time, and they have yet to disperse to look for food. Finding a mate any later could be quite expensive and difficult to do. So, estrus is synchronized across all females and generally occurs after weaning.

Most cases of polygyny result in a sexual dimorphism, with the males being larger. In the elephant seal world, you have to be big if you want to be a successful male, right?

Actually, there is an alternative strategy known as sneaking. Sneakers tend to be smaller, agile, and quicker males; they wait for a large male to become distracted and sneak in and inseminate as many females as possible before quickly leaving. Sneaking is not a particularly successful strategy, but it is seen in many polygynous systems.

Cetacean Mating

◇ But what about the case of cetaceans, where the process is fully aquatic? Here the challenge is to have some way to bring individuals of the species together in what is, after all, a very big ocean. Certainly, those animals that reproduce seasonally appear to have breeding grounds that are often separate from the feeding grounds.

◇ Feeding grounds can sometimes be unsuitable for breeding due to their generally colder temperatures. It is unclear whether breeding grounds are biologically defined—that is, the animals have some specific biological needs that are only fulfilled by a

particular environment—or culturally defined—that is, animals return to the same breeding ground again and again because it's what their mothers always did.

- Perhaps it's a combination of both of these mechanisms. Nonetheless, reproduction appears to be at least one of the driving forces in the process of migration. Females nearing parturition move toward warmer, typically more sheltered waters.

- The main reasons for this movement appear to be twofold: to provide an environment suitable for a newborn calf that will be particularly susceptible to the cold and to provide an environment relatively free of predators.

- The migratory cycle is typically tied to the seasonality of the feeding grounds. In this way, the feeding ground will be, in theory, at peak productivity when the calf reaches it. The gestation period for most whales is therefore around a year, to synchronize with that cycle.

- Birthing in cetaceans is a little different from the experience of marine mammals that are tied to the land. The fetus presents tail first to maximize the length of time it remains connected to the umbilical cord, which snaps at the last minute, and the calf instinctually rises to the surface for its first breath, sometimes aided by other conspecifics.

- Because cetaceans are not tied to the land for birthing, the process of nursing is also a little different. First, mechanically it is quite a challenge. The mother appears capable of pumping the milk from one of the 2 teats on either side of the genital slit. Calves must be quite dexterous in establishing a hermetic seal with the nipple. Little is known about how they do this; we have very few close-up visual accounts of the event.

The fat content of marine mammal milk is highly variable between species. It is most concentrated in the phocids, containing around 50% fat. Otariid milk, by comparison, has maybe half that amount. Cetacean milk is around 35% to 40% fat. The award for fattest milk goes to the hooded seal at 60%.

- Second, the nursing period is much more extended in cetaceans than in any other marine mammal species. As a comparison, most phocids will wean in a period of weeks, while otariids typically nurse for months. Cetaceans calves, however, may nurse for a year or more.

- In cases where the nursing period is extended, calves, pups, and mothers have to learn how to recognize each other. For land-bound marine mammals, this is probably done through a combination of smell and calling.

- In cetaceans, calves may roam freely away from the mother, but not too far. Mothers will often call, apparently for the return of the calf. When traveling, the calf often adopts a station by the mother where she can easily bump into the calf, confirming that it is still there.

- In certain species, especially dolphins, mothers will use signature whistles, calls unique to that individual, which are then mimicked by the calf. When a female calf grows to be an adult, it appears to use the same or similar signature whistle. In this way, calls can be used to trace heredity.

- Eventually, the calf will have fattened enough to take on the migration to the feeding grounds. Mother-calf pairs swim more slowly and are often both the last to leave a breeding ground and the last to reach a feeding ground. Most mysticete calves are approaching weaning by the time they get there.

- However, the mother-calf bond is the most stable association known in cetaceans and can last past weaning. Other groupings of whales that you might see on any one day will be random and more likely a function of prey distribution or some form of coordinated behavior.

- The actual act of coitus has only been observed in a fraction of cetacean species. Females can choose to try to deny a male by rolling on their back and leaving their genital slit exposed to the air or simply by just fleeing. This strategy only works according to how able the female is to either hold her breath or sprint away.

- Researchers have also observed cases in which males cooperate to corral a female. In many species, coitus involves multiple males inseminating a single female.

- In other species, it is less clear how mates get selected, or even if it is the male that selects the female or vice versa. Humpback males, for example, sing. And the fact that only the males sing implies heavily that the performance of the song has something to do with courtship, but exactly what is unclear.

- Following mating, most mysticete species disperse. Depending on the level of sociality, odontocete species may remain together. Then, around a year later, if the mating was successful, birthing occurs. For those species that migrate, birthing is linked to peak productivity at the feeding ground. However, for those species that are resident in one place year-round, mating and birthing is more asynchronous, presumably because productivity is less seasonal.

- Once a pup or calf weans and becomes independent from the mother, we class it as a juvenile. A juvenile really only has 2 jobs: stay alive and grow. At some point, it will become sexually mature, in which case we term it an adult. Age of sexual maturity varies among species and can be anywhere from 3 years and up.

Sexual maturity does not necessarily mean that the animal is ready to reproduce. Males, for example, often have to reach a particular physical size to compete with other adult males, and that may take some time beyond reaching sexual maturity.

- Fecundity of a female is also highly species specific. Long-lived animals tend to birth less frequently. While certain marine mammals, such as phocids, are quite capable of reproducing every year, large cetacean species need recovery time between births. This is probably because the acts of calving, pregnancy, and lactation are extremely costly for a female. This slow reproductive rate is an important factor when considering how to manage a population from the point of view of conservation.

Whaling records indicate that humpback females may lose as much as half their weight during the breeding half of their migratory cycle, only to regain that weight during their time on the feeding grounds.

LECTURE SUPPLEMENTS

Readings

Berta, Sumich, and Kovacs, *Marine Mammals*.

Evans and Raga, eds., *Marine Mammals*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Reynolds III and Rommel, eds., *Biology of Marine Mammals*.

Questions to Consider

1. Broadly compare life histories of whales and dolphins. What are the similarities? What are the differences?

2. For the semiaquatic pinnipeds, nursing mothers may choose to remain on the beach with their nursing young or take the odd trip to stock up on food. Identify a species example of each of these strategies. What adaptive differences do they have that help them in these 2 strategies?

3. Broadly identify the different mating strategies in marine mammals (monogamy, polygyny, etc.). What are the advantages and disadvantages of each? Find an example species for each.

22

BEHAVIOR AND SOCIALITY IN MARINE MAMMALS

This lecture will explore some of the wonders of marine mammal behavior. Behavior is one part of the sum total of how an organism meets the challenges of the environment, the other part being the adaptive physiology and morphology of an organism. In the broadest sense, we can divide those challenges into 6 categories: How is food acquired? How are mates acquired, and what is the process of reproduction and parental investment? How is competition handled within and outside the species? How do members of the species interact socially? How are predators avoided? How do species coordinate movement and migration around the ocean?

Acquiring Food

- Foraging techniques are quite diverse within the marine mammals but can be loosely grouped into those animals that chase individual prey items versus those that filter-feed on large schools of smaller organisms, such as schooling fish or plankton.

- Most marine mammals choose the former strategy: With the exception of certain pinnipeds, filter-feeding is the exclusive domain of the baleen whales. Sirenians form a third group that might be classified as grazers, as this clade is exclusively herbivorous.

- We now know that odontocetes—toothed whales—have the ability to use echolocation to interrogate their environment, and thus they presumably use this ability to forage for prey. Echolocation clicks are organized into sequences known as click trains, and the interval between clicks is often used to diagnose the state of the hunt.

A searching dolphin will tend to issue slow click trains. However, once prey is found and the dolphin acoustically focuses in on the target, the click train increases in rate, and the hunt is on.

- In some areas where they have been studied consistently for decades, we also know that dolphins can locate fish visually, especially if visibility is good. However, in the river dolphin groups, visibility is often very low, so presumably the species rely more heavily on echolocation to find and acquire prey.

- Many dolphin species appear capable of coordinating hunting behavior between individuals to help corral prey, and this is the first good reason for a marine mammal to be social: Perhaps being part of a group increases the chance of successful prey acquisition.

- However, we must always consider the benefits against the costs of a decision. Feeding groups may become more successful with greater group size, but this also increases competition between individuals for the catch. This is likely an important factor in limiting the size of a group.

Why should one whale help out another? It's a dog-eat-dog, ruthless world out there, and we expect individuals to act selfishly. Outside of humans, there appear to be very few instances, if any, of true altruism—the act whereby an individual will provide a benefit to another at the donor's cost.

- We can evaluate behavioral choices by the long-term benefits they provide. Ultimately, it's about survivorship, choosing the behavior that best ensures the passage of genetic material on to the next generation. If a foraging behavior isn't worth it, the forager won't adopt it.

Acquiring Mates

- In marine mammals, polygyny—a mating system whereby a male will attempt to sire as many offspring with as many females as possible—appears to be the rule. How males attract and maintain mates is species specific.

- In semiaquatic species, such as Stellar's sea lion, where parturition is tied to the land, males may choose to defend a desirable haul-out site that then attracts females. This is known as resource defense, and in this situation, it is the female making her choice of haul-out site, breeding with whatever male happens to be defending it.

- In a variation on this, males might defend access to prospective females, a behavior known as female defense. In this instance, there are 2 options: defend the female throughout the breeding season to ensure that the defending male is the only successful inseminator or defend her only during the process of mating.

- However, in fully aquatic environments, territories are less likely and the animals are much more mobile. Therefore, resource defense is not typically observed. Female defense in the water is also much more difficult—for a solitary male to deny access to a female from all possible directions would be difficult—so in the rare instances when it occurs, it is usually because of alliances that have been set up between multiple animals, as we see in bottlenose dolphins.

- What seems to be more common in aquatic situations are opportunities to lek, whereby males advertise their fitness to females and females then make the choice of mate. One explanation of humpback whale song is as an advertisement of fitness to listening females.

- In any of these systems, the role of the male beyond insemination appears to be very minor, except in cases where males help defend a group against predators. In cases where that group potentially contains offspring of that male, then that would count as a form of male, or paternal, investment. But in general, paternal investment is very rare.

- Also, especially if members of a group are related, there is the potential for shared parental responsibilities among females. Sperm whales, for example, forage at great depths, so mothers must be away from their calves for a long time. By having asynchronous dives, some females can remain at the surface and tend to the young of other females. This is known as alloparental care.

- Like group hunting, alloparental care is an example of reciprocity, whereby animals take turns looking after a crèche of young. If the animals are related, then that would mean that the babysitter was investing in inclusive fitness, because her charge would be related to her and therefore would share some of her genotype.

Competition and Sociality

- As a rule, any organism will seek to avoid or minimize competition, and the type of competition it can most easily control is intraspecific competition—that is, competition with other conspecifics for the same resources. In fact, this topic aligns well with the question of sociality.

- Do we move as a herd, or pod, or do we become solitary? This is a question that has been addressed by every marine mammal, through the process of evolutionary ecology. As with other instances of behavioral choice, the answer to this question lies in which strategy results in the best gain in inclusive fitness.

- The advantages to being solitary or minimally social are clear. Intraspecific competition is minimized. You only have to be worried about yourself. You don't need to defend others, nor do you need to share resources.

- But there are also challenges. When the time comes, how do you find a prospective mate? And there are a whole host of processes that are more easily performed by a group, including the search for food, maintained vigilance for a predator, and the opportunity for alloparental care.

- In this regard, researchers refer to the selfish herd. This theory proposes that there are 3 immediate advantages to grouping up:

    1. By becoming part of a pack, one has immediately reduced the probability of being taken as prey, as the predator now has multiple animals to choose from.

    2. Predation risk is decreased because multiple prey options might confuse the predator.

    3. More in the pack means more pairs of eyes and other senses detecting predators.

- Looked at in this way, it makes sense to group up. But there are costs to this, too. More in the group means greater competition for resources and potential aggressive interactions.

◇ In general, actual fighting between conspecifics is a last resort. Fighting can be costly, perhaps carrying the ultimate cost of death. Instead, we see a series of scaled cues that are designed to help animals bluff their way to dominance without the need for an actual fight. This is known as a graded response. That said, fights do occur; males often bear the scars to prove it.

◇ So, does a mammal go it alone or work as part of a group? The answer will be the result of an audit between costs and benefits on an individual basis. Mysticetes, for example, require such large amounts of prey that it rarely makes sense to rove in groups larger than a few animals. There are some exceptions to this rule—for example, in the case of cooperative feeding behavior.

◇ It's also perhaps important to point out the difference between a socially defined group that chooses to operate as a unit versus an aggregation of animals that are located in geographic proximity because of some resource. In either case, you would see the same thing—a group of animals densely clustered in a particular geographic area—but in only one of those cases is there a social bonding within the group.

◇ Because of water's excellent sound conducting properties, individuals do not necessarily need to be in visual range of each other to constitute a social grouping, as long as acoustic contact is possible.

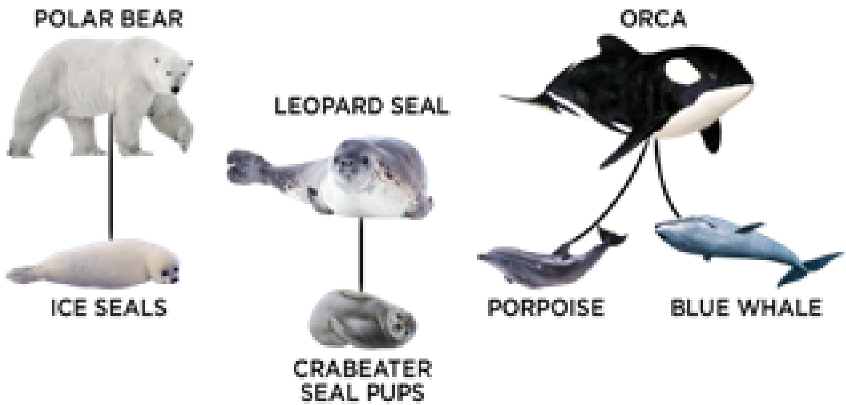
◇ Odontocetes, on the other hand, are more variable in their response to the question of sociality. Long-term studies have demonstrated that certain species of dolphin have a fission-fusion society, with alliances constantly being formed and broken. The only bond that seems comparatively stable is the mother-calf bond, where the benefits of gregariousness seem clearer, including group foraging and vigilance.

Beluga whale (*Delphinapterus leucas*) mother and calf

◇ The immense sperm whale—the largest of all toothed whales—does something somewhat in the middle of the spectrum of sociality. Females group together in pods of about 10. Calves are born into these pods, but somewhere between 5 and 10 years of age, the males leave their maternal pod to join roving bachelor groups. These groups get smaller as the animals get older, and once the males become sexually mature, they will meet up with female groups temporarily for the purposes of mating. Otherwise, the adult males are quite solitary.

Avoiding Predators

◇ Because of their size, most marine mammals have few predators, other than humans. Three marine mammal species act as apex predators in various food webs, eating a diet that in part includes other marine mammals: The polar bear frequently takes various ice seals, the leopard seal will occasionally prey on crabeater seal pups, and the orca can prey on anything from a porpoise up to a blue whale. These 3 apex species have very little to fear from any other predator other than humans.



- In general, most adult mysticetes are too large to be preyed on successfully, although accounts of orcas hunting as packs and successfully killing calves are more common. In those cases, the mother will typically try to help defend the calf with flicks of the tail. Otherwise, their only hope is to outswim their aggressors. Sometimes this works; sometimes it doesn't work. The orcas' strategy, in turn, is to wear out the calf and weaken it through blood loss, until the calf can be drowned by forcing it underwater.

- In general, the smaller a marine mammal is, the more vulnerable it is to attack, both from apex marine mammal predators as well as large shark species. But in all of these cases, one of the most important keys to avoid being eaten is to spot the predator in time to affect an escape. And so, we come back to one of the advantages of being in the herd: increased vigilance. This is doubtless at least one of the reasons why the smaller odontocetes are much more gregarious, as are the pinnipeds during critical phases of their life history cycle—for example, when birthing and breeding.

Minke whales seem particularly vulnerable to orca attacks. In fact, in the Southern Ocean, there appears to be an orca ecotype that is entirely dedicated to preying on minke whales. The minke whale's behavioral strategy to avoid being eaten appears to be to hide, to avoid being seen in the first place. Southern Ocean minke whales are very cryptic in their swimming behavior and along the Antarctic Peninsula will often hide in the pack ice.

Migration

- Thus far, we have assumed that the physical and biological environment is relatively stable. In reality, it is not. Productivity is often seasonal. Polar regions become quite inhospitable in the winter. Predators might be more common in certain areas at certain times of the year.

- Because of this, animals might choose to migrate. For a humpback whale to invest the enormous amount of energy required to migrate thousands and thousands of miles on a yearly basis, there has to be a reason. And once the fitness audit is in, the investment of all that energy to migrate is justified by the benefits that accrue from migration.

LECTURE SUPPLEMENTS

Readings

Ford, Ellis, and Balcomb, *Killer Whales*.

Mann, Connor, Tyack, and Whitehead, eds., *Cetacean Societies*.

Mulvaney, *Ice Bear*.

Stirling, *Polar Bears*.

Whitehead, *Sperm Whales*.

Whitehead and Rendell, *The Cultural Lives of Whales and Dolphins*.

Questions to Consider

1. Why do you think that breeding behavior in marine mammals is tightly linked to birthing?

2. Can you think of examples of cultural transmission of information in species other than marine mammals and humans?

3. This lecture discusses 3 different ecotypes of orca. In fact, there are several more. Investigate the remaining ecotypes and the differences in their diet.

4. Why do you think that examples of cooperative foraging behavior are so rare? Under what circumstances do you think it might evolve?

5. How do sperm whales defend against orca predators?

23

MARINE MAMMAL DISTRIBUTION AROUND THE GLOBE

Marine mammals have been successful in occupying the various available ecological niches of the ocean. This lecture will focus on that success by taking you to many ocean regions to examine the diversity of habitats that marine mammals have conquered. All marine mammals are highly mobile and will tend to live in areas that provide the resources they need, which perhaps most importantly includes access to food, although it can also include particular kinds of geographic environment.

Distribution of Semiaquatic Species

- ◇ All marine mammals are certainly aquatic, but they do not necessarily live in an aquatic environment all the time. Semiaquatic species—such as the marine otters, pinnipeds, and polar bears—are in part tied to the land, and even within those clades, there are differences in the degree of land dependence. So, in these instances, we must also consider the suitability of the coastline associated with the ocean habitat.

- ◇ Sea otters, for example, unlike their riverine kin, spend most of their time in the ocean, often associated with kelp beds that provide a habitat within which they can both hide and hunt.

- ◇ Within the pinnipeds, phocids are more aquatically adapted, yet they will often haul out on land to rest, or to avoid marine predators, or for reproductive purposes. Otariids are more terrestrially adapted than their phocid cousins, but they are still superb swimmers and quite at home in the water. They use the land in a similar manner to phocids. In both cases, males will often develop territories on land that can then be used to attract females.

- ◇ Suitable haul-out territory differs between species, but there are often commonalities. Haul-out sites are usually isolated, often away from human activity, but frequently on small islands that are free from terrestrial predators, such as foxes. Access to the water should be easy, and sheltered areas are often preferred. That said, haul-out sites can often be tidal, with prime habitat disappearing underwater at high tide.

- ◇ Despite only being semiaquatic, the pinnipeds are indeed superb swimmers, and some are excellent divers. So, it would be incorrect to think that their land dependence makes them poor performers in the water.

An interesting example of haul-out selection is the use of subantarctic islands, such as South Georgia, by Antarctic fur seals. At this latitude, there is no other land for hundreds, maybe thousands, of miles. So, these islands become focal points for haul-out sites. In the 18th and 19th centuries, pioneering sealers discovered these haul-out sites and flocked in the hundreds to collect their bounty: the much-prized coat for which the fur seal is named.

- Another example of a land-based marine mammal is the polar bear. Polar bears are intimately tied to the sea ice of the Arctic, where they find their prey: seals. While they will occasionally come to land and sometimes forage on berries when no other food is available, for the most part they live on the sea ice and can potentially have immense ranges or territories, over thousands of square kilometers.

- Again, just because the polar bear presents itself as a terrestrial quadruped, don't be fooled into thinking that it's no good in the water; polar bears must frequently swim between broken-up ice floes in the search for their prey. In the course of several days, a polar bear can easily swim at least a hundred kilometers, perhaps more. This is an ability they may need to rely on more as the ice continues to diminish in the high Arctic.

Distribution of Cetaceans and Sirenians

- ◇ Because they are herbivores, sirenians, or sea cows, are confined to shallow coastal areas, where there is enough marine vegetation on which to forage. This often brings them into estuarine or swamp-like areas that are more brackish in nature. However, with the exception of the Steller's sea cow, which has been extinct since around 1770, sirenians appear to favor warmer waters greater than 15° Celsius, so for the most part are restricted to a tropical or subtropical distribution.

- ◇ Cetaceans are highly mobile, so we might expect them to demonstrate the broadest ranges in distribution, and indeed this does appear to be the case. For the most part, cetacean distribution appears to be linked to the distribution of their prey.

- ◇ Mysticetes, or baleen whales, for example, are filter feeders, taking fish and squid occasionally, but most often feeding on plankton. Because plankton drift with the currents, we look to oceanographic causes to help explain the distribution of plankton, which then in turn also help us predict the distribution of feeding of baleen whales.

- ◇ Planktonic distribution is far from homogenous across the ocean and in fact is strongly associated with oceanographic forces that cause hot spots—so we also see baleen whales in such areas.

- ◇ Perhaps the best example of this is the so-called polar or Antarctic convergence. Whales gather in this region to feed because local conditions create an oceanic front that traps the plankton. That the front is conveniently located near certain human-occupied subantarctic islands made for a rich scenario for prospecting whalers.

- Most baleen whales are not adapted to dive deep because they do not have to. Their prey is typically found close to the surface, so, while we find mysticetes in geographically diverse areas, they are not usually using the entire water column unless an area is particularly shallow. These shallower areas over the continental shelf are referred to as the neritic zone.

- There are certain odontocetes, however, that are extremely well adapted for deep diving, and for that reason we will find them in areas of deep water, off continental shelves and over trenches and deep-sea canyons, searching for deepwater squid—the beaked whales and sperm whales. It is thus unusual to find these species close to shore, unless the bathymetry gets very deep very quickly. Of all cetacean species, these deep divers probably have the most oceanic, or pelagic, distribution.

White-beaked dolphin (*Lagenorhynchus albirostris*)

- Smaller cetacean species may be more challenged by colder environments; because of their size, they lose more body heat per unit volume when compared to larger animals. So, we tend to see many of the smaller odontocetes, including most dolphins, in tropical, subtropical, and temperate regions.

◇ There are some notable exceptions, however. Certain dolphin species seem capable of surviving in subpolar or boreal climates; these include the white-beaked dolphin, as well as hourglass and right whale dolphins. These may also be classified as having a more pelagic, rather than neritic, distribution. These species make their living by roaming far and wide for local, short-term hot spots of food productivity.

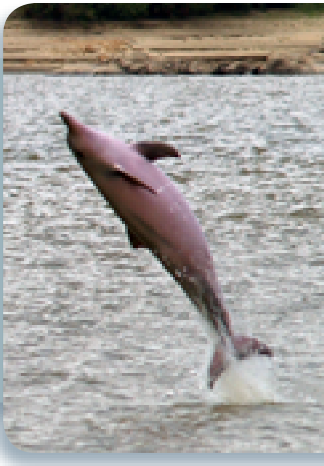
◇ Orcas are perhaps the most pan-globally distributed of all cetaceans. As apex predators, they are often at the top of marine ecosystem food chains around the world. Interestingly, it appears that orcas have, within their species, created specializations in their diet. In some cases, orcas have developed techniques to hunt one kind of prey that are incompatible with techniques to hunt other kinds of prey.

◇ As a result, different diet specialists, or ecotypes, do not intermix or interbreed, and over thousands of years, they have become genetically isolated from each other—to the point that they are considered subspecies, and perhaps even new species. This process is called speciation, and in this case, it appears to be happening because as apex predators, food is very limited, and thus a degree of resource partitioning makes sense.

◇ Some odontocete species appear to be exclusively neritically distributed—that is, you will only find them in waters over the continental shelves. Most species of porpoise, for example, are typically found very close to shore.

◇ A few marine mammal species—specifically, one species of manatee, one species of seal, and several species of dolphin—may not be found in the ocean at all but instead in certain river or lake systems. These species are the Baikal seal, which is endemic to Lake Baikal in Siberia; the Amazonian manatee, which is distributed throughout the watershed of the Amazon river; and 4 species of river dolphin.

Because of its proximity to various indigenous tribes in South America, a dolphin species known as the tucuxi has special significance. Local tribes believe the animal to be a shapeshifter that can take on the form of a handsome male human. All dressed in white, the dolphin-man will gate-crash village celebrations and seduce the women in the tribe—and possibly even conceive illegitimate hybrid offspring. Most anthropologists suggest that the myth could be a cultural mechanism to explain and justify pregnancy out of wedlock.



Migration

- In the North Atlantic, a humpback whale will travel from its breeding ground in the Caribbean to a more northerly feeding ground. Such movement is in the order of thousands of kilometers, and it is appropriate to refer to this as migration.

- While at a feeding ground—for example, the Gulf of Maine—it might move between specific points of productivity. This we would call commuting. It might decide to move to a different feeding ground altogether; that movement would be called ranging. At the end of the feeding season, the whale would then migrate back to its breeding ground. Thus, migration is a semiannual phenomenon.

- In this sense of the definition, not all marine mammals migrate. Some remain highly localized year-round, likely because their habitat provides adequate resources regardless of the season.

- Sirenians, for example, typically do not migrate. All that a West Indian manatee needs is right along the shores of Florida and the Caribbean: warm water, abundance of vegetation for foraging, sheltered bays to reduce predators, and so on.

- But some marine mammals do migrate and, in some cases, over extraordinary distances. Reasons to migrate might include thermoregulatory concerns, especially for calves or pups that would be especially challenged in cold waters due to their size. Another reason might be avoidance of predators during particularly vulnerable stages of life history—for example, during parturition and nursing.

- A humpback whale, for example, only remains at a feeding ground for perhaps 3 to 4 months, perhaps less for feeding grounds found at higher latitudes, where the seasons are noticeably shorter.

- Because a 15-meter humpback whale has to open its massive mouth and mobilize a multiton tongue as a hydraulic press to produce a reasonable meal of prey, there are only relatively few places in the ocean, often those places with nutrient-injecting upwellings, that are on the A-list for a humpback that needs to feed.

- Implicit in this idea is that for the remainder of the year's cycle, the whale will be in areas that are not capable of such productivity. And while any wild animal will likely take food wherever it can get it, if a humpback moves to warmer, sheltered waters more suitable for birthing, nursing, and subsequent mating, then it must face the consequence that calorific opportunities are going to decline.

- Many marine mammals work through this problem using a fasting strategy that is aided by the fact that insulating blubber can also be used as a source of energy. A humpback whale, for

example, may lose a significant amount of body weight during the breeding ground fast. Mothers that birth that year have the added stress of milk production, so females may stand to lose as much as half their body weight over the winter.

- ◇ Losing so much weight over the winter really underscores the importance of finding adequate food reserves in the summer. Humpbacks often return to the same feeding ground year after year, a behavior known as philopatry, or site fidelity. They return to these places probably for 2 reasons: It is very likely the site they were first taken to as a calf, and over evolutionary time, on average, the site has been productive enough to sustain that humpback's need for calorific gain.

- ◇ However, sometimes the ocean does not provide. In the southern Pacific, there is an oceanographic cycling known as the El Niño/Southern Oscillation. During an El Niño year, productive upwellings are suppressed, and productivity in the region is substantially lowered. There is a similar cycling in the North Atlantic known as the North Atlantic Oscillation, which also affects productivity in feeding areas such as the Gulf of Maine or the productive waters surrounding Newfoundland.

- ◇ In such years, humpbacks may switch feeding areas—what we would call ranging. A recent study found that poorer productivity often resulted in lower whale residency. Simply put, not being able to find their needs in their traditional feeding ground, the whales moved elsewhere.

- ◇ The pattern of migrating back and forth between low latitudes and high latitudes is a common theme in mysticetes. Whales will spend the summer in a high-latitude feeding ground and then migrate to lower latitudes for the purposes of breeding and reproduction.

The current migration record is held by a gray whale that traveled 22,511 kilometers in the course of 172 days, from eastern Russia to Baja and back again.

◇ How do marine mammals that engage in such long migrations know where they are going? How do they know they have arrived? How do they know when to go? We simply do not have the answers to these questions, although 3 interesting hypotheses have been suggested. In each case, the proposed migratory cue must work over scales similar to the huge distance that some of these animals achieve.

1. Whales use the relative position of the Sun in the sky as a crude form of celestial navigation.

2. They use some sort of magnetic cue. While a fascinating idea, we have yet to discover an organ involved in the detection of magnetic fields.

3. They use sound. Given most marine mammals' extraordinary hearing abilities, is it possible that long-distance migrators can "hear" acoustic landmarks?

OLD BLUE

At the end of the Cold War, the U.S. Navy offered the use of its submarine listening stations to certain U.S. marine researchers. They were drawn to a recording of a blue whale, known to the navy as Old Blue, who vocalized a particularly idiosyncratic moan that could be tracked by triangulation stations up and down the U.S. Eastern Seaboard.

Over the course of 43 days, Old Blue traveled from just south of Cape Cod, down to Bermuda, then to Florida, and then back to Bermuda—a voyage of almost 2500 kilometers, across an open ocean apparently devoid of any landmarks.

How did Old Blue know where he was going? Some have suggested that perhaps he was using the reverberations of his low-frequency moan, which has the potential to travel vast distances, bouncing off targets and echoing back to the whale.

LECTURE SUPPLEMENTS

Readings

Evans and Raga, eds., *Marine Mammals.*

Parsons, *An Introduction to Marine Mammal Biology and Conservation.*

Stirling, *Polar Bears.*

Questions to Consider

1. It's recently been documented that during the austral summer, some Antarctic killer whales will perform quick (around the scale of weeks) migrations to the warmer waters of South America before returning to the Antarctic Peninsula to forage. Why do you think they do this? To research this, go to https://www.livescience.com/16723-antarctic-killer-whale-migration.html.

2. Larger bodies proportionally tend to lose less heat than smaller bodies per unit volume. Given this generalization, can you predict the distribution of marine mammals given the latitudinally controlled changes in ocean temperature? Are larger animals found in colder regions and smaller animals in warmer regions?

3. What adaptations does the Weddell seal possess to survive year-round in a polar environment?

4. Sperm whales and blue whales are frequently found feeding in the Gulf of California, which is located paradoxically in a subtropical zone. What accounts for the unusually productive waters of this region?

INTELLIGENCE IN MARINE MAMMALS

So much myth has built up around marine mammal communication and intelligence that many people have somewhat skewed perceptions about it. The goal of this lecture is to cut through the mythologizing and determine what contemporary science has to say about intelligence in marine mammals. The jury is still out, and the question of whether a marine mammal is intelligent very much depends on your definition of intelligence. That said, these animals don't need to be smart to earn our respect as complexly adapted organisms capable of living in the mysterious and hostile ocean environment.

Communication and Intelligence

- Within evolutionary biology, communication is defined as the process by which a signal is provided by a transmitter with an intent to manipulate the actions of a receiver in a way that will improve the transmitter's inclusive fitness—which is the ability to pass down one's genetic information to future generations, directly through one's own progeny or indirectly through relatives.

- This definition of communication serves to justify why an animal might evolve an ability to communicate. For example, warnings shouted to one's children out of concern for their safety clearly maximizes a sender's fitness by ensuring the offspring's survival from that threat.

- It is no coincidence that a human's maximum audio frequency sensitivity is centered around the frequency of a baby's cry; in this instance, one might say that the baby, or transmitter, is manipulating the receiver—the parent—into providing attention. In turn, increased parental vigilance increases the chance of the infant's survival.

- Many anthropologists and philosophers would say that humans *do* use communication in different and more abstract ways, and indeed, that is part of being human.

- But a basic biological definition is our best entry point for examining communication and intelligence in marine mammals. It helps us frame scientific answers to 3 questions that, in one form or another, people tend to ask about these creatures: Do marine mammals communicate in such a way that implies intelligence? Are marine mammals so intelligent that they can learn to communicate with us? Given the answers to the first 2 questions, are marine mammals at least as intelligent as we are?

Q & A

Q: Do marine mammals communicate in such a way that implies intelligence?

A: There are a myriad of examples that demonstrate that marine mammals are capable of tasks and behaviors that we would associate with higher brain function and cognitive awareness.

Q: Are marine mammals so intelligent that they can learn to communicate with us?

A: Marine mammals communicate, but they probably use communication in a way that's completely different from the ways we do. If language exists in a marine mammal species, it is probably based on entirely different premises in comparison to human language.

Q: Given the answers to the first 2 questions, are marine mammals at least as intelligent as we are?

A: This is the wrong question to ask. If we define intelligence as the ability to solve problems using innovative behavioral solutions, then we can agree that marine mammals are intelligent. But they are a different kind of intelligent—not measurable on any scale devised by humans so far.

- ◇ Do marine mammals communicate intraspecifically—that is, within the species? Absolutely. Do they communicate in a sophisticated manner? That depends on your definition of sophistication, but it appears that communication can be pretty sophisticated.

- ◇ For example, sperm whales emit series of clicks known as codas that differ in their quality between certain groupings of animals. And the examples are not limited to sound: Male elephant seals have a series of graded body-language behaviors designed to settle a fight before it starts, and many otariid species use smell to confirm the identity of a pup.

Sperm whale (*Physeter macrocephalus*)

- Whether this type of communication can be used as evidence of intelligence depends on your definition of intelligence. Psychologists have some pretty formulated ways of measuring human intelligence. IQ, or intelligence quotient, is often used as a comparative scale to assess human intelligence. Marine mammals score extremely low on an IQ scale. But that doesn't mean that they aren't intelligent; it could just mean that we are using the wrong scale.

- The concept of applying an IQ test to a dolphin seems ridiculous and pointless. Hopefully, this shows how our third question misses an important point. People may want to compare human intelligence with marine mammal intelligence. But intelligence isn't a single, homogenous capability. There are different kinds of intelligence, and they are not any more comparable than apples and oranges.

- Instead, it would be more appropriate to think about how an animal stores and processes information. An "intelligent" response would be one whereby an animal reacts and uses information to improve its chances of survival. Some responses might be more sophisticated or complex than others.

The Brain

- ◇ The notion that marine mammals must be intelligent because their brains are so large is a much-touted misunderstanding. In fact, marine mammal brains are large because their bodies are large and therefore require larger brains to coordinate their physiology and behavior.

- ◇ More useful, perhaps, would be a way of expressing the size of the brain relative to the body it controls. This ratio is known as the encephalization quotient (EQ), and it is a ratio—expressed as a percentage—of brain size to body size by weight and therefore normalizes the measure relative to the size of the animal.

- ◇ However, researchers still debate what weight we should use as the quotient in this ratio as well as whether we should adjust for the fact that larger animals need larger brains. So, the following EQs all use the same standard, which adjusts the ratio allometrically; in other words, it takes into account the size of brain we might expect for a given weight.

- ◇ Humans have the highest known ratio, at around 7.5%. Dolphins have an EQ of around 4% to 5%. Most baleen whales have EQs approaching 2%. Chimpanzees are around 2.5%, dogs are just over 1%, and horses are just under 1%. Average EQ for mammals is around 1%. However, be careful placing these along a scale of smart to intellectually challenged.

- ◇ Looking in more detail at the composition of the brain, all marine mammals have extensive development of the cerebrum, the area thought to be associated with higher brain functions, such as memory and cognition. However, the cerebrums of dolphins and sperm whales are much more infolded than those of baleen whales, resulting in greater surface area and providing perhaps more areas where neural networking can occur.

- Also, the limbic and paralimbic systems are quite substantial in the brains of whales and dolphins. In humans, these areas of the brain are associated with processing emotion. Could these brain systems help promote the unusually high levels of sociality we see in certain marine mammal species? It's a tantalizing question, but more research needs to be done before we can reach a definitive conclusion.

Observations of Cognitive Function

- Based on observation, cognitive function in certain marine mammal species appears to be high. Some are capable of tool use. For example, sea otters use rocks to break open particularly resistant bivalves.

- Bottlenose dolphins, together with orcas and false killer whales, appear capable of recognizing their image in a mirror. This is a very rare ability that is seen only in humans, magpies, macaques, chimpanzees, orangutans, and Asian elephants. Being able to recognize one's own image is a first step toward the concept of self, something we humans take for granted but that is apparently largely absent in the animal world. Some marine mammals may be self-aware.

- Many marine mammals are trainable. At marine parks, animals are often trained to put on shows. Specific behaviors are performed in the show because of subtle cues provided by the trainer. Training of this kind is performed through a technique known as positive operant conditioning, whereby the trainer rewards the trainee whenever a correct behavior follows a learnable cue, such as some form of hand gesture or auditory signal. This is possible with a variety of marine mammal species that can be kept in captivity.

- The public are mostly aware of captive facilities and marine parks designed for edutainment. However, certain scientific institutions, as well as the U.S. Navy, also have captive facilities, where operant conditioning is used to help us understand the workings of marine mammals better.

- Some of these facilities have performed extraordinary work, including demonstrating that bottlenose dolphins are capable of understanding language rules—in others words, syntax. That is not to say that dolphins possess language as we understand it or the syntax within it; rather, they can be taught rules on which human communication is based. In a seminal paper in the mid-1980s, researchers demonstrated that dolphins could be taught to understand the concept of verbs and objects.

- The ability to be trained in these ways—to learn rules—indicates possession of a higher cognitive function. But this is all in captivity. In the wild, creating experimental conditions is very difficult; instead, we must rely on correlational observations. Nonetheless, researchers believe that they have documented some extraordinary instances of learning. Perhaps the most impressive of these is the apparent presence of culture in certain marine mammal species.

- In the animal world, culture has a very specific meaning: variation in behavior within a population as a result of social learning. Bottlenose dolphins, orcas, and humpbacks—all with encephalization quotients higher than 1—have been used as examples of animals that use social learning, sometimes referred to as cultural transmission, to pass on certain behaviors.

- The extraordinary behavior called strand feeding is where an orca will deliberately beach itself and snag an unsuspecting sea lion pup and then roll and wriggle back into the surf and the safety of deep water. How this behavior was initially developed, we do not know. But we do know that the behavior is apparently being passed down to future generations through cultural transmission, apparently through females that will "teach" the behavior to the young.

- Our strongest evidence for cultural transmission appears to be between individuals that are related. For example, recent evidence suggests that sponge use in bottlenose dolphins is a behavior passed from mother to daughter, in what is referred to as vertical cultural transmission. Lateral cultural transmission occurs, too, whereby nonrelated individuals adopt a new behavior, although it is more difficult to explain this in terms of fitness and may be more a case of mimicry of an actor by an observer.

- Finally, the use of play behavior, as seen in many marine mammal species, is an indicator of intelligence. Play behavior may have many functions, but most researchers agree that it is an excellent low-investment method of practicing behaviors that in the future may be critical for survival and for gaining muscular strength and coordination.

Even though the juvenile play form of a behavior might be very similar to the adult form, juveniles seem to know when the behavior is real and when it is just play.

Elephant seal weanlings chew on each other and rear up together in imitation of what the mature 4-ton beachmaster males do. Yet while the latter can result in serious injury, for the pups it does seem to be just play. Perhaps there is some kind of signal at initiation that says that what follows is play.

◇ Humpback calves and juveniles are often seen playing. Perhaps one of the most impressive behaviors seen in any cetacean species is breaching, in which an animal will leap either completely or partially out of the water, slamming back down against the surface to spectacular effect.

◇ Why whales breach is unknown, although there are several possibilities. Some have shown that the resultant slap against the water produces an acoustic signal that transmits for kilometers and therefore could be a response to another whale's breaching activity. Some believe that breaching may be a whale's attempt to dislodge parasites from its skin. Others believe that it is a sign of aggression. Finally, some believe that it could just be play. In reality, it is probably all of these—and perhaps more, depending on the context of the situation.

LECTURE SUPPLEMENTS

Readings

Brakes and Simmonds, eds., *Whales and Dolphins.*

Mann, Connor, Tyack, and Whitehead, eds., *Cetacean Societies.*

Muth, "Crows Take a Look in the Mirror."

Whitehead and Rendell, *The Cultural Lives of Whales and Dolphins.*

Questions to Consider

1. What benchmarks do you personally use to determine if someone is intelligent? How useful would those methods be in measuring animal intelligence?

2. Using the Internet, research the experiment known as the mirror test. How does it work? How do we know if the animal has recognized its own reflection?

3. What are some of the other uses of play behavior? Can play ever be just for fun, or do you think that is a function that is reserved for humans only? Or does play behavior, even in humans, always have a deeper motive?

4. Do you think that marine mammals can be considered intelligent?

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THE CHARISMATIC MEGAVERTEBRATES

Marine mammals are sometimes referred to as charismatic megavertebrates. Whether justified or not, the Western public seems to have elevated these species, resulting in having a deep, almost spiritual, reverence for these animals. This lecture is about the changing relationship between humans and marine mammals. You will discover that over the millennia, Western attitudes toward marine mammals have moved from resource exploitation to conservation. In the East, however, resource exploitation remains an important theme.

The History of Humans and Marine Mammals

- Our first contact with marine mammals likely goes way back, before we ever kept records of such things. Based on findings from midden heaps, we know that various North American native tribes depended on small marine mammals as a source of sustenance. And marine mammals play an important role in native culture.

> Certain northwestern native tribes revere whales, which are considered to represent strength and power.

- The Ancient Greeks, and later the Romans, certainly mention marine mammals in their writings. Dolphins especially seemed to be revered and were often the subject of local folklore. Pliny the Elder writes about dolphins in his encyclopedic work *Naturalis historia*, perhaps borrowing from Greek authors such as Aristotle.

- Perhaps one of the most well-known representations of a whale comes from the biblical story of the reluctant prophet Jonah, who ends up being swallowed by a leviathan, or "great fish," which most people interpret as referring to a whale. By the time of the printing of the King James Bible, whaling would have begun in earnest, and stories would have abounded about the dangerous hunt for the great leviathan.

- Just before this, the Swiss naturalist Conrad Gesner had revived Pliny's and Aristotle's work on natural history. In his 1551 publication *Historiae animalium*, Gesner created a bestiary that combined his own work with that of his predecessors.

- The section on whales is of great interest and includes a 3-panel illustration that depicts interactions between humans and whales. The whale pictured is extremely caricatured. One can see evidence of an operculum, or gill flap; a decidedly fishy tail with raylike spines for support; stalked blowholes; paws for flippers; sharp teeth; and a stocky body that is reminiscent of a short, fat crocodile.

- Gesner's work would have been published at a time when the Basque people of Spain began whaling in earnest. At some point, we realized that a dead whale could be valuable—for its blubber as a source of oil, for its flesh as a source of food, and for the baleen and teeth. And the Basques of Europe very much led the charge to take advantage of these resources.

- By the 16th century, the Basques were extremely effective and competent seaworthy folk. Without so much as a steam engine—that would take another 250 years—the Basques began the decimation of whale stocks, aimed largely at North Atlantic right whales.

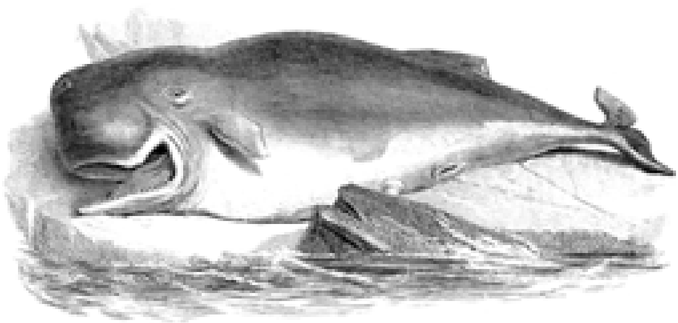
North Atlantic right whales (*Eubalaena glacialis*)

- Other marine mammals were hunted during this time, most notably seals. Although native tribes had been hunting seals for sustenance for probably thousands of years, the first Western attempts to commercialize the hunt began in the 16th and 17th centuries, coincident to the English settlement of Newfoundland, where harp and hooded seals were common. While stocks appear to have crashed occasionally, seal populations in this region seem fairly resilient, and a hunt continues to this day.

- Another marine mammal hunted at this time did not fare so well. The Steller's sea cow, a giant manatee valued for its flesh, became extinct around 1770 because of unsustainable hunting.

- Our next cultural milestone, and the next whale celebrity that loomed large in the public's eye, was Moby Dick. Published in 1851 by Herman Melville, *Moby Dick* is a collage of Melville's experiences hitchhiking around the Pacific aboard whaling vessels, together with an apparently true story about a large sperm whale that destroyed the whale ship *Essex*. Melville then took all of this and created the fictionalized Captain Ahab and sailor Ishmael aboard the *Pequod*.

- The story of *Moby Dick* is rife with all kinds of fascinating information about what it meant to be a 19th-century whaler. Through Melville, we finally understand that there is nothing particularly romantic about whaling. It's gory, the stench is unbelievable and relentless, and it is dangerous.



- The story of *Moby Dick* occurs within what historians refer to as the Yankee whaler period—a time when Nantucket was the center of commercial whaling. Technically, though, this era was before the Industrial Revolution, so whaling was relatively inefficient compared to later decades of the 19th century.

- With the Industrial Revolution came access to greater technologies and better building techniques. Ships became more powerful, safer, and capable of hauling massive weights, such as whale carcasses. Thus was born the industrial whaling period, which reached its peak in the 1910s through the 1930s.

- During the industrial period, whales—and, in fact, marine mammals in general—were further objectified as resources that, once dead, could be used for the betterment of humans. Not only were many whales slaughtered and pushed to the edge of commercial and biological extinction, but so were the sea otters and some pinniped species for their fur and the northern and southern elephant seals for their blubber.

The Unsustainability of Hunting

- From the 19th century to almost the middle of the 20th century, the whale hunt was conducted with only minimal regard for long-term consequences. In fact, just before the turn of the century, Thomas Huxley, an important ecologist of the time, had declared the oceans "inexhaustible." Thus, few seemed to think, or perhaps even care, that the marine mammal bounty of the 19th and 20th centuries was unsustainable.

- But unsustainable it was, and by the 1950s, it was clear that something was terribly wrong. No one could find whales to kill anymore. At this time, international whaling efforts were governed by the International Whaling Commission (IWC), which created a Scientific Committee in 1950 that then began the onerous task of assessing the status of various whale stocks around the world.

- By the 1960s, the results of those investigations were coming in, and the news was not good; several species were immediately protected from further hunting. Parallel to this was the growing environmental movement, and the plight of the whale was taken up by many as the epitome of what humans were capable of doing in their ignorance.

- All kinds of information was flying around, with little to confirm it as truth or rumor, including that odontocetes were being used by the navy for military purposes, cetaceans were sentient beings, dolphins were being slaughtered as bycatch in tuna nets, pilot whales were stranding in masses on our shores, and pollution was killing our planet.

- In the United States around this time, 3 pivotal acts were read into the legislature: the Clean Air Act of 1970, the Marine Mammal Protection Act (MMPA) of 1972, and the Endangered Species Act of 1973. Each of these recognized our role in protecting the resources of the planet and in some cases placed stringent laws of protection around certain species.

Because of the Marine Mammal Protection Act of 1972, all marine mammals in U.S. waters and on U.S. shores are protected, regardless of their endangered status. In this way, this act is an excellent example of our willingness, as a society, to give marine mammals distinct status.

- Also in 1972, the United Nations proposed a moratorium on whaling, a call that was echoed by many countries. In 1982, enough votes were achieved for the IWC to invoke the moratorium, but not without considerable politicking. Finally, in 1986, the whales—for the most part—got their respite.

- How did other marine mammal species fare? The hunt for sea otters for their luxuriant fur was stopped in the 1910s on realization that the populations were becoming commercially extinct—a term applied to a population whose numbers are so low it that is no longer commercially viable to hunt them and is often a warning that extirpation of the species is imminent unless immediate action is taken.

- Various species of fur seal are now similarly protected, as is the elephant seal. For the most part, this kind of protection is provided on a country-by-country basis. For example, the MMPA protects all marine mammals in the United States, but it has no bearing on creatures elsewhere in the world. It's only the IWC, bound by international treaty, that has a more global impact.

- Some species are still hunted. The Newfoundland seal hunt continues, apparently sustainable but not without controversy. And certain countries, such as Japan and Norway, continue to hunt whales using bureaucratic loopholes. But while a few species are still close to extinction because of humans, most seem to be slowly recovering.

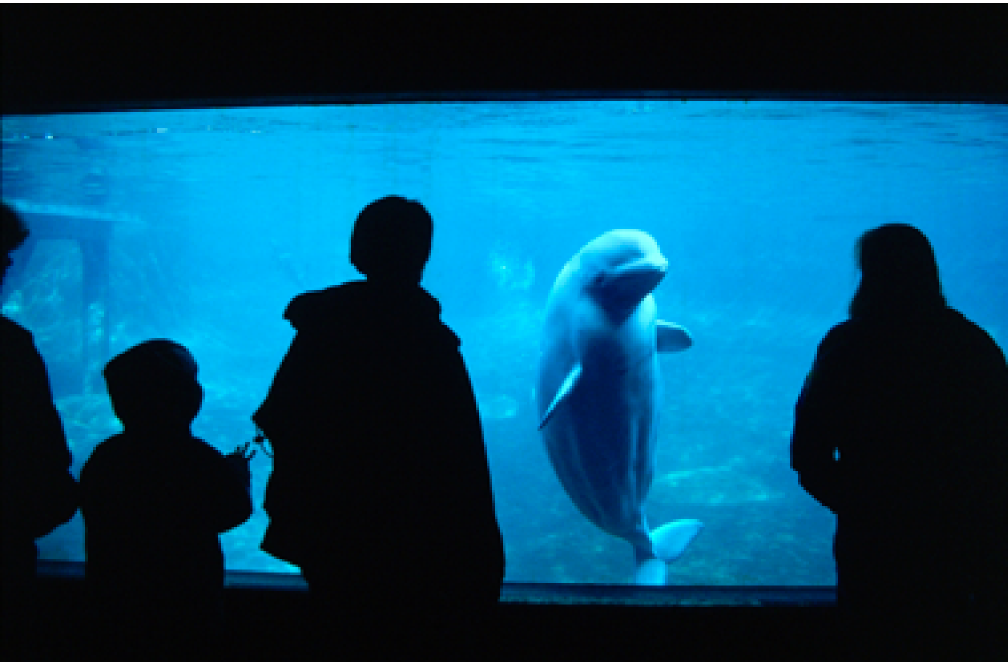
In 2016, most of the world's humpback whale populations were delisted from the endangered species list. This is applauded by many as a sign that our conservation strategies are working, at least for some species.

Whale Watching as an Industry

- In the past 40 years or so, we have seen the emergence of whale watching as an industry. In the 1970s, someone figured out that whales could be just as valuable as living, breathing specimens as they were dead on a whaling ship. Today, whale watching is a multimillion-dollar industry.

- At its best, whale watching can inspire people to care and can teach people about these extraordinary creatures. At its worst, whale watching can stress animals and reinforce stereotypes by providing incorrect information.

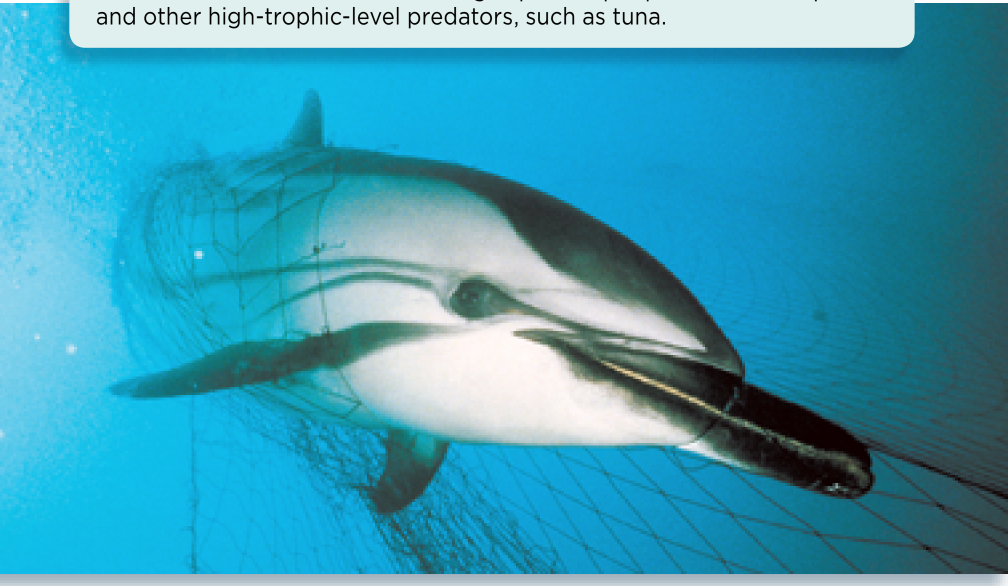
- If popular culture is an appropriate gauge of public opinion, then our fascination with marine mammals appears to be deepening, with popular movies such as *Free Willy*, *Dolphin Tale*, *Orca*, *Whale Rider*, and even *Star Trek*.



◇ While most of the popular culture is fairly harmless, there are many very good documentaries that provide the public with a fuller understanding of marine mammal life history and act to dispel some of the myths that have arisen around them. There are also excellent accounts of the changing relationship between humans and marine mammals.

◇ The 2013 documentary *Blackfish* tells the tale of the impacts of captivity on orcas. The story focuses on one particular whale, Tilikum, who killed 2 trainers and allegedly a third member of the public who broke into the facility after hours and was found floating dead in Tilikum's pool.

The dolphin meat that comes from the slaughter of dolphins is poisonous. Dolphins, as high-trophic-level predators, accumulate toxins—such as mercury—in their flesh. Anyone who consumes that flesh then also takes on that toxic burden, and there are credible accounts of increased levels of dementia among Japanese people who eat dolphin and other high-trophic-level predators, such as tuna.



- The film made a strong case that the claustrophobic conditions under which we keep orcas, animals that are used to roving thousands of miles, are inhumane, and experts cite this as the lead reason that caused the psychotic episodes that resulted in the 3 deaths. The current owner of Tilikum, SeaWorld, was severely criticized for its role in the tragic deaths.

- SeaWorld subsequently announced an entirely new direction for its orca captivity program. In 2016, the company reached the decision that they would no longer acquire or breed orcas. The animals at SeaWorld now will be the last generation to be held in captivity, and they will live out the rest of their lives in new pools designed to better emulate the wild environment. Whether or not other captive programs will announce a similar policy has yet to be seen.

- *The Cove* is a 2009 documentary of an undercover operation that sought to expose a dolphin herding operation in the Japanese town of Taiji. In this operation, hundreds of dolphins are herded and trapped in a particular cove. A few are selected for captive programs throughout the world. The rest are slaughtered for their meat.

- Through the course of the film, the story of what actually happens at "the Cove"—which allegedly is kept highly secret to even to most of the people in Japan—is slowly exposed, and once film footage is obtained that confirms the deed, the filmmakers take it to government officials for their reaction. The film ends with the filmmakers taking their evidence to the IWC, although it is unclear if it has any effect there.

- The herding and slaughtering practice continues to this day under much tighter security, so the practice of the dolphin slaughter is even harder to monitor. As a documentary designed to reveal a covert practice, *The Cove* succeeded; as a documentary designed to stop the slaughter, so far, it has failed.

LECTURE SUPPLEMENTS

Readings

Cowperthwaite, *Blackfish*.

Hargrove and Chua-Eoan, *Beneath the Surface*.

Klepac, ed., *The Whale's Companion*.

Martin, *The Whale's Journey*.

Melville, *Moby Dick*.

National Oceanic and Atmospheric Administration, "The Marine Mammal Protection Act."

Philbrick, *In the Heart of the Sea*.

Psihoyos, *The Cove*.

Society for Marine Mammalogy, "The Society for Marine Mammalogy."

Twiss Jr. and Reeves, eds., *Conservation and Management of Marine Mammals*.

Questions to Consider

1. How is a hunt for seals or whales—for substances such as oil and flesh—any different ethically from our exploitation of the domesticated cow and a hunt for deer?

2. In the United States, what rules protect whales from encroaching whale watch vessels? Are these rules different in other countries?

3. Get a group of friends together to watch the movie *Blackfish* and organize a postviewing discussion on whether we should keep killer whales—or any marine mammal—in captivity.

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THE GREAT WHALE HUNT

This lecture is about whaling and sealing, practices that still go on today but at nothing like the scale they did in the past. Whaling and sealing are those acts whereby we deliberately kill an animal for the purposes of exploitation. The kill either happens out in open water or on ice, or animals are driven from open water into shallow bays, where people wait to slaughter the animals, a practice known as drive hunting.

Whaling and Sealing

- We have been hunting marine mammals for a very long time. Based on evidence from their middens, the Maritime Archaic Indians took marine mammals 9000 years ago. They used barbed weapons and developed the first-known toggle harpoon, a device that once implanted rotated its point so it could not be pulled out. Designed perhaps to catch within the fascia between blubber and skin, or blubber and muscle, this tool might also have been used to catch small odontocetes, such as porpoise.

- Our first nonnative commercial attempts to take seals began around 1500 A.D. Various countries began to seal in earnest, especially in eastern Canada and Newfoundland, then a colony of Great Britain. Commercial whaling predates commercial sealing by several hundred years thanks to the European Basques, a race of people that will be forever identified with whale hunting; records are unclear and controversial, but there is evidence that the Basques may have been whaling as early as the turn of the first millennium.

- Hunts for seals and whales were essentially looking for the same materials: flesh to eat and blubber to render to oil. Additionally, seals provided pelts that could be used to make leather and fur products, and whale yielded what was known as whalebone, which was an early reference to the baleen plates of a mysticete whale, not actually true whale bone. Baleen could be used for a number of products, such as umbrella stays, corset supports, and lampshade ribs. It would be the 20th century before whalers figured out ways to use real whale bone as a viable product from the hunt.

- Other than the challenges of the environment, sealing was initially a relatively simple trade. The types of seals taken in the 16th century were typically nonaggressive and relatively easy to approach and spear. In contrast, the Basque whalers targeted for the most part North Atlantic right whales, animals that are notoriously strong and capable of aggression.

- Among the Basques, the hunt began with observers along the shoreline looking for migrating whales. Boat teams would then be notified, who would row out to the whale.

- The first part of the actual hunt involved harpooning the animal. Contrary to popular belief, the harpoon's job was not to kill the animal, but to attach a length of line, to which various buoyancy devices could be added that would create drag against the whale's attempt to swim and dive.

- Once the whale had tired sufficiently, the boats would then approach the animal and stab it to death. So, the animal died from blood loss—far from a humane death. This could potentially take hours, during which the boat team was at risk from the violent actions of the animal's death throes. Once dead, the animal was towed to shore for processing.

- ◇ Above all other tissues, the blubber was particularly prized, so care was taken to strip, or flense, that material first using axes and sharp knives. Strips of blubber were put into large cauldrons known as try-pots and were rendered down in a soupy solution of freshwater. The rendered oil was then decanted off into barrels and used for the most part as a medieval fuel.

- ◇ Although the process sounds horrific and disgusting, the Basques must have been very brave and accomplished as mariners to kill a 15-meter whale from a small rowboat. And although the process sounds quite artisanal, it was also highly efficient; it was not long before local whale populations had been extirpated and the Basques had to take to sailing ships, roaming the open ocean.

- ◇ Eventually, whaling companies were started in other countries, often using the Basque people as consultants or laborers. In Europe, the English, French, Dutch, and Danish were important in the whaling story. As stocks became more depleted locally, whalers pushed out farther and farther, looking for the new mother lode. For several centuries, whaling was highly competitive, and fleets were frequently protected by each country's navy.

- ◇ Sealing, in the meantime, was also becoming a successful enterprise. Expanding from Canada, sealers started to look at the potential of the Southern Hemisphere, using various islands within the sovereignty of their flag nations as bases. Whaling and sealing often went hand in hand; whalers were known to take the odd seal as a change of diet from rations onboard the ship or in the camp.

> One could make an argument that our discovery of new lands in the far north and south was driven in part by our hope to find new stocks of whales and seals.

Improvements to the Industry

- As ships became more and more capable, whalers and sealers could push farther south and north. Based out of Nantucket and New Bedford, vessels would traverse Cape Horn and the Cape of Good Hope into the Pacific and Indian Oceans, areas as yet relatively untapped, carrying their fleet of harpoon rowboats. By the 18th century, the fishery had become global.

> The Yankee whaling fleet, of which Herman Melville writes in *Moby Dick*, was capable of voyages of 2 to 3 years.

- In addition, technologies had improved to the point that whalers could now try for the mighty sperm whale—the best prize because of the spermaceti oil the animal yielded, an oil of extraordinarily fine quality. Whalers perfected a technique borrowed from the Basques known as the Nantucket sleighride, whereby the chaser boat would attach itself, by longline, to the harpooned animal. The boat would be towed for miles before it could approach the exhausted animal for the final kill.

- However, toward the end of the 1800s, humans were pushing farther south again. Earlier that century, the Antarctic continent, with all its untapped bounty, had been discovered, and the race was on. Countries that already had flagged islands in the area had a head start. Thus, Great Britain, with the Falkland Islands and South Georgia firmly under its belt, had an important advantage.

- At the turn of the 20th century, Britain began granting licenses for companies wishing to start up processing plants on these islands, and there was much money to be made through these lease agreements. Islands such as these provided prime access to marine mammals that used the polar convergence as a feeding ground.

- Two other important developments primed the industry for its heyday in the first half of the 20th century: Ships became steam-powered, more capable, and therefore farther-ranging; and killing methods had become more and more refined.

- With the decline of right whales, whalers were now looking to target the much-faster rorquals. And while various projectile methods of delivering a harpoon had been used by this point, it was through the efforts of the American Thomas Roys in the 1850s and the Norwegian Svend Foyn a few decades later that the cannon-delivered explosive harpoon was developed.

- This gun was mounted onto fast, steam-powered catcher ships. The animal would be killed by the concussion of the blast, or through the sheer severity of the wound, and pulled up to the side of the vessel by a steam-powered winch. It would then be injected with compressed air that would keep the carcass afloat while it was towed to a processing station, such as Grytviken on South Georgia.

- Many whalers also exploited the South Shetland Islands and the Antarctic Peninsula, a little out of the way from South Georgia, which would have been the closest island with processing plants. So, while a whaling station was established on Deception Island in the South Shetlands, whalers also started to use vessels anchored in protected coves as a base of operations.

The jawbones of whales were often taken by whalers to use as gateposts back home.

- However, as is the case in many boom-and-bust industries, people became greedier. Britain kept raising its license fees to the point that companies, particularly Norwegian companies, needed to find a better solution. And they found it in the factory ship, a vessel so large it could process multiple whales, from carcass down to the bone, within an hour. Now, catcher vessels simply had to bring their whale to a local factory ship, which made their hunt more efficient, too—they could stay out for longer.

- The whale would be transferred to the factory ship, and aided by a stern ramp, it could be winched onto the deck by a scissor caliper. Flensing could begin almost immediately. First, the skin and blubber were taken. Then, the carcass could be winched to the next area of the deck, where the meat would be flensed from the bone. Finally, the bone itself would be broken up into smaller chunks by steam saw. All of this was done with aid of huge winches that could pull bits of the whale in different directions.

- Different parts of the whale would then be pulled by lemmers, a particular class of whaleman, into giant holes in the deck that led to massive onboard boilers, the modern equivalent of a try-pot. There would be a system of boilers for each of the different grades of tissue, resulting in different grades of oil.

- Factory ships were likely the final nail in the coffin for whale populations. The whaling process had become so efficient that it simply was not sustainable. Yes, there were lulls in demand, especially as petroleum-based products became more available, but newly discovered chemical processes, such as saponification, allowed whale oil to be used in a more diverse array of markets.

Management

- There was very little management within the whaling industry. The attitude of the time was that the oceans' resources were unlimited, and the whaling industry in the early 20th century thought no differently. However, by the 1930s, it was clear that something was amiss, and whales were becoming harder to find.

- In 1946, a group of nations signed the International Convention for the Regulation of Whaling. At last, here was a mechanism whereby nations could coordinate their management practices globally to prevent overhunting. The convention recognized the issue of "overfishing," and its first action was to convene the International Whaling Commission (IWC), a group that to this day is responsible for the global management of whale stocks.

- The IWC developed a Scientific Committee, and recommendations for a global moratorium on whaling occurred as early as 1972. The official implementation of that moratorium happened in 1986.

- Even after the moratorium was established, the IWC language permitted nations to object to the decision of a moratorium. Notable among these nations were Norway, Japan, and Russia. Japan later withdrew its objection after pressure from the United States and thus became bound by the moratorium. Norway, however, did not and resumed minke whaling in 1993. Their practice of whaling continues to this day, and they suggest that it is a sustainable hunt.

- In the meantime, a new management group has been started by pro-whaling nations called the North Atlantic Marine Mammal Commission (NAMMCO). Signatories include Norway, Iceland, Greenland, and the Faroe Islands, home to a pilot whale drive hunt that has existed for hundreds of years. Although NAMMCO touts itself as an "international regional body for cooperation on the conservation, management and study of cetaceans and pinnipeds in the North Atlantic," it is also clearly an organization made up of pro-whaling states dedicated to the resumption of legal whaling.

Long-finned pilot whales (*Globicephala melas*)

- The IWC has its critics, most of whom say that the commission has no teeth. Those same critics note that in spite of improved management methods, whale populations have not recovered in the way that was hoped. The IWC seems mired in politics, yet it remains our best hope for a global coordination of research that can lead to the sustainability of whale stocks.

ON THE HUNT

There are nations that still hunt, or want to hunt, whales, some believing that it can be done sustainably. And although sealing is very much reduced, it still happens in certain countries—particularly Canada. They, too, claim that the hunt is sustainable, and with seal populations in the several millions, it's hard to argue with them.

Yet we have proven, time after time, that in the long term, we as a species seem incapable of sustainable hunts, be they fish, whales, seals, or buffalo. This seems especially relevant as marine mammal populations do not have the capacity to recover as quickly as other hunted species.

Readings

Dolin, *Leviathan*.

Ellis, *Men and Whales*.

Estes, DeMaster, Doak, Williams, and Brownell, *Whales, Whaling, and Ocean Ecosystems*.

Kalland, *Unveiling the Whale*.

Twiss Jr. and Reeves, eds., *Conservation and Management of Marine Mammals*.

Questions to Consider

1. Research the history of the International Convention for the Regulation of Whaling and the birth of the International Whaling Commission. What were the principles behind the Revised Management Procedure?
2. Within the context of the current whaling moratorium, under what provision may one still whale?
3. Consider the mandate of the International Whaling Commission. Do you think that the commission has been a successful endeavor?
4. What are the similarities in management errors that lead to a whale population becoming commercially extinct and a fish population becoming commercially extinct?
5. Research the criticisms of Japan's scientific whaling program.
6. List the goal of a fishery manager. (Hint: Sustainability is not the only choice here, nor in our current economic climate is it necessarily considered the most important).

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THE EVOLUTION OF WHALE RESEARCH

The difficulty of figuring out aspects of a cetacean's life history is mostly due to the fact that we only interact with most marine mammals for the brief instants that they are at the surface to breathe. Otherwise, they disappear into their aquatic realm. In this lecture, you will discover techniques that have shed light on the mysteries of whale life as examples of the broader study of marine mammal research.

The History of Marine Mammal Research

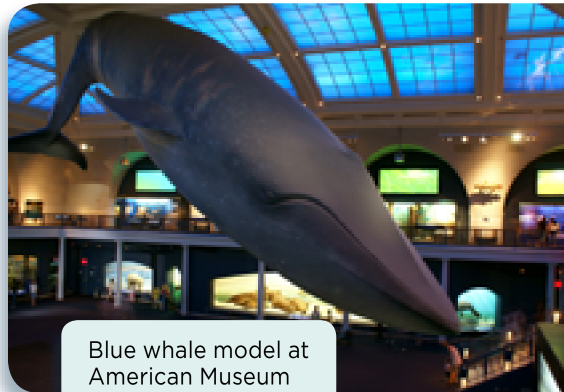
- Aside from early natural historians who might have had the odd opportunity to dissect an animal that had washed up on shore or who had spent time observing behavior—particularly of those species that are semiaquatic—the first real advances in marine mammal science came from the years when marine mammal hunts were prevalent. These hunts would often give an interested viewer access to the carcass, and by helping to dismantle the animal, much could be gleaned.

- When whaling and sealing became commercially scaled, then our knowledge of the animals became more secure because we had access to large numbers of carcasses. This introduces an important concept in science: individual variability.

- Among a group of humans, there are variations in sex, age, hair color, height, body mass index, skin color, and other features as determined by ethnicity. If we were to sample just one person and say that person is representative of the entire human race, we would be doing our race an injustice. We capture the extent of that diversity by taking a statistical sample; in other words, we measure many subjects instead of just one and represent the variation through averages and error bars around those averages.

- Having access to multiple carcasses yielded from a hunt allowed us to be more confident about what we knew of marine mammals because of the statistical trends that began to emerge. Important practitioners in this time were morphologists, who would measure the dimensions, masses, and proportions of anything and everything in the body, including the complete skeleton, and attempt to make sense of why a body was designed as it was.

◇ As the whale hunt gained steam in the late 19th and early 20th centuries, the great natural history museums of the Western world were coming into their own: The British Natural History Museum moved to its current location in 1881, overseen by paleontologist Richard Owen; the American Museum of Natural History opened its doors in 1877; and the Smithsonian National Museum of Natural History opened its doors in its current location in 1910. For all you see in the public exhibits of their lofty halls, there are countless specimens behind closed doors that help define what we physically understand about a species.



Blue whale model at American Museum of Natural History

◇ Understanding a marine mammal's behavior was often key to finding it and killing it. While not necessarily scientifically trained, whalers knew how to find whales through experience, and some of the early whale scientists had strong associations with the whaling industry, or used it as a source of data.

◇ As whaling and sealing passed through their heydays in the early 20th century, we started to know much more about the different species of marine mammals and their distribution. Darwin's theory of natural selection, and the modern evolutionary synthesis that derived from it, provided us mechanisms through which we could understand adaptation.

◇ However, our work with live animals was largely constrained to surface interactions. That began to change as we emerged from World War II, when new techniques came into play that allowed us to study cetaceans not just as carcasses but as living creatures.

- For example, development of technology such as scuba in the 1940s helped us penetrate the underwater barrier—though to this day scuba is surprisingly underutilized, because most marine mammals appear to be intimidated by the bubbles produced by the aqualung and therefore stay away.

- But there were other technologies that arose from the 2 world wars—technologies that had a huge impact on the aquatic sciences. Not only did boats become safer and farther ranging, but we also developed a technique to look into the water column: sonar.

- Sonar was an important development that allowed us to understand the habitat in which we found marine mammals—the nature of the seafloor, or topography, for example—as well as the presence of fish schools upon which the marine mammal might be feeding.

- However, sonar is not particularly useful in observing the marine mammals themselves. The search beam generated by shipbound sonar tends to be very narrow, so it cannot be used to track an animal. Also, marine mammals tend to be very sensitive to the frequencies used by sonar, so they will tend to avoid it. In fact, certain types of sonar are harmful to marine mammals, so we tend to avoid its use unless one can use it in noninvasive ways to characterize prey fields or bottom topography.

- For the past half century or so, marine mammal science has taken a 2-pronged research approach. First, where possible and permissible, we have kept animals in captivity and trained them to help us research particular scientific questions. This approach has also allowed us to conduct what might be defined as true experiments, whereby a subject is manipulated or exposed to a treatment in a very controlled fashion and all confounding variables are eliminated or accounted for.

- In a second approach, we examine and observe animals in the wild, or in situ. In this strategy, true experiments are often not possible because we cannot control what happens to the animal. Rather, we observe while the animal goes about its life. This kind of research design is sometimes referred to as correlational design, whereby we measure the animal and a range of other variables important to the animal and we associate them.

Captivity Research

- Keeping animals in captivity for the purposes of experimentation is now a highly controversial practice, but much of what we understand about physiology and energetics in marine mammals comes from this kind of study. While many members of the public object to any animal being kept in captivity, in reality research facilities are highly accountable to the conditions that their captives experience.

- Many such facilities are not open to the public but are still regularly inspected and operate under strict permits and standards. If the facility cannot maintain these high standards, then it often will be closed down, and the animals will be either released or moved to other facilities. Some facilities are also open to the public and must therefore respond to even higher benchmarks.

- Often implicit in this kind of work is the fact that only certain animals can be kept successfully in captivity. Thus, captive scenarios are often limited to pinnipeds, small odontocetes, sea otters, sirenians, and, in a few limited cases, polar bears. Those animals that lend themselves well to captivity are often used as models for other marine mammals.

> With one brief exception, a mysticete has never been kept in captivity. The exception is 3 grey whale calves that were kept sequentially in the 1960s and 1970s, the first dying and the latter 2 being released once they grew too large.

- Implicit in this kind of operation is that animals are often trained, through positive operant conditioning, to cooperate in an experiment. For example, to examine energy budgets, a sea lion might be trained to swim in an exercise pool that provides a constant water current. The air spaces above the pool are sealed off so that researchers can monitor oxygen uptake and carbon dioxide production.

- In a very few cases, experiments may be more invasive and might require biopsy of tissues. For example, we may be interested in hormone or stress levels or some other chemical measure of the animal's physiology. Typically, the more invasive the experiment, the more stringent the required permit.

- At a point somewhere between captive and in situ studies, trained animals are permitted free reign of the open-water environment but choose to return to captivity at the end of the experiment, mostly because of the knowledge of guaranteed food rewards. In many ways, this type of captive scenario seems to represent the best of both worlds: A degree of control is possible, but the researcher is measuring response to the real, rather than artificial, environment.

In Situ Research

◇ In situ studies—that is, ones that occur in the wild—are often considered to be the best option not only ethically, but also because they are the least invasive. However, in situ studies often have logistical challenges. We have to go where the animal is, and that often means a trip in a boat, sometimes to very hostile climes. Unlike the true experimental situation, we also have to accept that we might never know why an animal does what it does. We may have measured something that we think controls an outcome, but there's always the chance that we missed something.

> We still don't actually know why an animal breaches, a behavior that is often observed in situ. We have several very plausible explanations, but we don't know for sure.

◇ Moreover, while we can comfortably observe the animals when they are hauled out or when they are at the surface—as we sit in our boat or land-based blind—the minute the animal goes below the surface, observing the animal becomes much more challenging.

◇ The answer to this problem lies in the tag. A tag attached to an animal dives with that animal and experiences that dive. In this age of electronics, tags have various sensors and recording devices, and we can get all kinds of information about whale behavior. Perhaps the simplest form of electronic tag is the time-depth recorder. A pressure sensor onboard the tag measures the depth as the animal dives. When the data is retrieved, we can obtain a dive profile, allowing us to understand more about diving behavior.

- Tags are becoming more and more intricate with the miniaturization of electronics. With the DTAG, for example, one can tell the orientation of the animal in the water column at any one time. The device is so sensitive that it can pick up tail strokes and therefore has been incredibly useful in swimming behavior studies.

- Working close to an animal has always been an issue for researchers. It is often undesirable to be too close because that might harass the animal. Also, the animal's very behavior might be affected, thus nullifying any data we might collect. Tags offer us a way to travel remotely with the animal, and for the most part, tags do not appear to change the behavior of the animal.

◇ Another ingenious way to follow an animal, with presumably minimal disturbance, is to use a drone. The use of drones is still somewhat controversial, and if flown too low, a drone can indeed harass an animal, so the permitting process is still extremely strict. However, drones have been used to get excellent overhead footage of animal behavior—for example, bubble-net feeding.

Drones have even been used to fly through the blow of a whale, collecting important information about stress hormones that are coincidentally exhaled. Such a drone is delightfully referred to as a SnotBot.

◇ There are other ways to collect information about the biochemistry and physiology of an animal in situ with fairly minimal disturbance. For example, it is possible to collect scat from the animal—even from the fully aquatic whales, because it floats for tens of minutes before being dispersed. Scat contains important information about the animal's prey and can also be used for hormone analysis.

◇ We have also developed methods of taking a biopsy from free-ranging animals. Biopsy darts are typically delivered by crossbow or air gun. The tip of the dart is hollow and on impact samples a small amount of skin and perhaps blubber about the size of a pencil eraser. A rubber washer at the end of the corer forces the dart to bounce back out of the animal, and because the dart is buoyant, it can then be easily retrieved. Samples obtained in this way can then be used for molecular analyses, stable isotope and fatty acid analysis, and hormonal analysis.

- In the process of photo-identification, photographic images are used to capture external features of an animal that are unique to that individual. By photographing the animals, year after year, we also build up an account of their life histories. Photographic records have given us insight into breeding intervals and even longevity.

- All of this is done by comparing photographic images to a catalog of previously identified animals. Up to this point, the process of matching photographs has been extremely labor intensive, because nothing can match the human eye and brain in matching individuals. However, recent breakthroughs in image-recognition software are changing the game and will be a huge help, especially in the case of some of the larger databases.

The underside of a humpback whale's tail, together with the trailing edge of its fluke, can be used to identify an animal in the same way we might use fingerprints to identify a human.

◇ As our technologies improve, we will doubtless learn even more about the secretive world of the marine mammal. We have gone from brief accounts of animals at the surface to taking journeys with them. In this way, we have been privileged to enjoy the briefest of glimpses into their fascinating dark and watery world.

LECTURE SUPPLEMENTS

Readings

Boyd, Bowen, and Iverson, eds., *Marine Mammal Ecology and Conservation*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Reynolds III, Perrin, Reeves, Montgomery, and Ragen, eds., *Marine Mammal Research*.

Questions to Consider

1. Use the Internet to find out about the SnotBot. What kinds of questions can we ask in research on whales with such a tool?

2. What is the science of photo-identification, and how has it helped in our understanding of marine mammals? As part of your research, look into the concept of mark-recapture methods.

3. How does amino acid racemization work?

4. What is the difference between a satellite- and a VHF-based telemetry tag? How do these differences help shape the type of research in which they are used?

5. What is a Crittercam?

6. How have various live-holding facilities (aquariums, etc.) helped in improving our understanding of marine mammal behavior and physiology?

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MARINE MAMMAL STRANDINGS

This lecture is about marine mammal strandings. It is often difficult to determine why a marine mammal strands. It is amazing, and scary, how far people are willing to go to rescue an animal, often endangering themselves. A stranding situation can be so overwhelming that we are incapable of saving the animal. Sometimes stranding response is more about managing the people around the animal to reduce its stress rather than managing the animal itself. Stranding events represent an excellent opportunity to educate the public about marine life.

Reasons for Strandings

- According to the National Oceanic and Atmospheric Administration (NOAA)—the federal agency responsible for coordinating marine mammal stranding response—a stranding is when a marine mammal is found on land, dead or alive, and if alive is not displaying typical on-land behaviors. Live-stranded animals are usually ones that cannot return to their natural habitat without help.

- Thus, a dolphin alive on a beach is clearly out of habitat and incapable of returning to the water; it would therefore be considered a stranding. A seal resting on a beach is not a stranding, because that is a typical behavior, and seals are usually quite capable of returning to the water on their own. A seal pup, however, that has been abandoned prematurely by its mother and just lies on the beach day after day getting more and more dehydrated and thinner and thinner would be considered a stranding.

Some beaches are sonar traps in the sense that because of the sediment type and angle of the seafloor, an echolocating dolphin might receive misleading information as to the environment ahead. While the dolphin might think it is getting deeper and moving into open water, in fact the beach might be getting shallower.

- In special instances, more than one animal might strand at the same time. These are referred to as mass strandings, and they are particularly challenging logistically.

- Marine mammals strand for a number of reasons, some of which have yet to be determined. Certainly, animals can get sick just as humans do, and animals die from disease just as we do. Sometimes, a dead or dying marine mammal washed up on a beach can be a perfectly natural result of old age, disease, or high parasite load. If the animal is dying, we should probably play no further role, unless it is to ensure the animal is not unduly stressed or suffering needlessly.

- There are some natural events that might cause multiple animals to strand. For example, there are certain kinds of natural algal blooms that are toxic when consumed. These are referred to as harmful algal blooms or, commonly, red tide.

- In these cases, marine mammals do not necessarily eat the algae; rather, they consume the herbivores that feed on the algae or the predators that feed on those herbivores. In this way, the toxic signal is biomagnified as it moves up the trophic chain.

- By the time it gets to the marine mammal apex predator, it represents a toxic, often fatal, dose. And if multiple animals are affected, then we may have a situation in which many of them strand—either already dead or very sick.

- Sometimes we suspect that marine mammals just make navigational mistakes and get lost. Certain areas around the United States that see multiple strandings year after year are probably geographically confusing to a marine mammal.

- In addition to natural causes of death, there are a number of ways humans can cause a marine mammal's death that might lead to it being washed up on shore or that might cause a live stranding.

Cape Cod in Massachusetts sees a high number of stranded animals every year, and in fact often experiences mass strandings.

- Humans may have unintentionally—or, in very rare cases, intentionally—harmed the animal to the point that it washes up dead or alive on a beach. Common causes of mortality or morbidity include vessel strikes and fishing entanglement.

- In the case of a vessel strike, an animal may either be hit by boat, causing blunt force trauma, or it may be cut by the skeg or propeller of an engine. Either can cause instantaneous or rapid death or, in even less humane situations, may lead to infections and necrosis.

- In the case of fishing gear entanglement, an animal encounters either working or ghost gear and becomes entangled. In some cases, the animal is able to shed the gear, but in more serious cases, the gear cinches around the animal tighter and tighter and often latches onto other gear. If wound tight enough, the gear can cut through the skin, blubber, and muscle—even abrading bone—as the animal swims. This leads to severe myopathy and often fatal infections that will kill the animal, which might then perhaps wash up on shore.

- Perhaps the animal has been exposed to pollution in some way, either chemical or acoustic. We are dumping a variety of toxic chemicals into our oceans that might have a chronic or acute effect on marine mammal health.

- Also, because of the importance of sound to marine mammals, anthropogenic production of excess levels of sound—for example, through exposure to either seismic surveying or military-grade sonar—can permanently deafen an animal. With its primary sensory system unavailable, a marine mammal might then make navigational mistakes that would cause it to strand.

- Mass strandings can sometimes be harder to explain. In some cases, it appears that a number of animals have all been exposed to a particular event—such as a viral or bacterial epidemic that has swept unchecked throughout a population—that will cause morbidity and mortality across the entire group.

- In other cases, especially in instances where the marine mammal of concern has high sociality, it may be just a few animals that are sick and injured and the rest have followed them on to the beach. In such instances, humanely euthanizing only the sick animals may cause the others to return to sea.
- Sometimes, rather than a mass stranding, we see a series of strandings, referred to as unusual mortality events. These are common among populations experiencing an epidemic of some sort.

STRADING IN NEW ZEALAND

In 2017, New Zealand experienced its third-worst mass stranding when more than 400 long-finned pilot whales stranded on a beach on Farewell Spit. Despite concerted efforts to refloat the animals several times, many of the animals died. This mass stranding took place over several days, and while it is estimated that about 200 animals died, responders now believe that at least that number also survived.

Long-finned pilot whales seem particularly susceptible to mass strandings in part because of the strong social bonds within the group; if one strands, then many seem to follow.

Why We Respond to Strandings

- At the most primal level, we respond to strandings because we care. Humans are a compassionate species and do not like to witness suffering. An important part of stranding response is dealing with a very upset public who want to see the animal helped. This is completely understandable and not to be discouraged. However, the public sometimes has a very unrealistic view about what can be done—hence the role of education and information dissemination at a stranding event.

- At a more pragmatic level, we often respond to strandings because we are legally required to. In U.S. waters, marine mammals are blanket-protected by the Marine Mammal Protection Act (MMPA) of 1972, regardless of their endangered status.

- When it was reauthorized in 1992, the act created the Marine Mammal Health and Stranding Response Program, requiring NOAA to coordinate stranding response throughout the United States and act as an archive and dissemination center for data collected from stranding events. From the MMPA's point of view, stranding response is very much about the collection of data and about using that data to ascertain the health of a marine ecosystem.

- The Marine Mammal Stranding Network has been an extraordinary source of data over the years it has operated. So much of what we know about marine mammals is because of what we have been able to glean through examinations of dead bodies washed up on beaches.

- ◇ Another reason to respond to a stranding event is because we can, and we should. Many will argue the moral imperative here—that we should respond to marine mammals in distress because it is a very humane thing to do, and it is certainly within our capability, and becoming more and more so as our technology and understanding improve.

- ◇ Some believe that we should respond to a marine mammal in distress if the cause of the stranding is anthropogenic in nature. Also, even though it will have very little impact on the population, some prioritize response to an animal whose species is listed as endangered, if only for the opportunity to accrue more data on that species—data that might help the species survive in the future.

- ◇ Some say, however, that marine mammal stranding response might not be doing the population any favors. By saving animals that have proven unfit for the environment, we may be guilty of reintroducing genes back into the gene pool that nature had already selected out as being maladaptive. In other words, we are interfering with natural selection.

- ◇ This is an interesting idea, although there is no evidence yet to determine whether we are weakening the gene pool. It may be that we save so few animals that they have very little impact on a large population. We need more time to analyze this hypothesis.

- ◇ Also, some are concerned about the potentially harmful impact on would-be stranding responders. Marine mammals, like many other animals, carry diseases that can be contracted by humans. The stranding response community handles this problem by adopting very high standards of safety and hygiene, and many stranding response institutions insist on their employees receiving regular inoculations against common diseases.

Stranding Procedures

- The procedures we follow when a marine mammal strands depends on whether the animal is alive or dead. If the animal is dead, a stranding response team will typically visit a carcass to collect the most rudimentary data: species, location, gender, and so on. All this assumes that enough of the carcass survives for us to make those determinations.

- Generally, we do our best to glean what we can from carcasses regarding soft tissues. Often, we will conduct a necropsy under sterile medical conditions in an attempt to ascertain the cause of death. This is where we can find important information about disease, parasites, and internal injuries. External injuries may be evident depending on the kind of injury. The skeleton can also be useful in determining cause of death.

Necropsy of smaller animals, such as seals and various odontocetes, is relatively straightforward. However, as the carcasses get larger, necropsies become more and more challenging. Individuals certified to necropsy large whales have to be familiar with local public health safety codes, emergency response systems, people management, use of heavy equipment, first aid, and data and sample collection.

- Once the flesh of the animal has been cut up, composting systems in the United States can render the very fatty flesh down to soil within months. We use a similar system to clean the flesh off the bones, which are then bleached in the Sun, cataloged, and archived for potential future articulation. Samples and other evidence from the carcass are next inspected to see if we can determine the cause of death. We often bring in veterinary pathologists and other specialists.

- If the animal strands alive, then there is an entirely different set of approaches, which depend in part on whether the animal is semiaquatic or fully aquatic by nature. If it's a seal, for example, and if we believe the animal can get itself out of the fix it is in, then usually we try to leave it alone and let Mother Nature decide. The animal may end up dying, but if it's a natural death that would have happened anyway—if we hadn't discovered the animal—then that's probably okay.

- If a seal is in a high-traffic area and is likely to be harassed by humans, then we can either establish a cordon and remain with the animal until it moves away, or we can relocate the animal to a quieter area. We are typically reluctant to relocate an animal because we don't want to move it away from an area where it is supposed to be—either because of food availability or the additional presence of a mother or pup.

- If the animal is sick, then we might consider whether it is a viable rehabilitation candidate. Although they are becoming increasingly rare and overcrowded because of funding issues, there are a number of rehabilitation facilities around the coast that might agree to take an animal, especially if the prognosis is good.

- If the seal is not a viable rehabilitation candidate, then we would typically euthanize the animal. This is done under strict medical conditions to ensure that the animal feels no pain. The carcass may then be necropsied to determine the cause of morbidity.

- If a small cetacean strands, the options are more limited. As soon as that animal hits the beach, it's out of habitat. We can either try to return the animal to the ocean, or we can euthanize the animal. In very rare cases, we might consider rehabilitation if a suitable facility exists, but those are very scarce. Transportation of a live cetacean is fraught with problems; the animal must be kept cool, wet, and well supported.

- Refloating the animal can be successful, but sometimes the animal will re-strand if still confused or sick. Euthanasia can be difficult, and becomes more so as the animal gets larger. If a large whale live-strands, one's options are limited, and euthanasia is extremely challenging. The dosage concentration required to euthanize a small whale is very lethal to a human, so extreme care must be taken.

LECTURE SUPPLEMENTS

Readings

Dierauf and Gulland, eds., *CRC Handbook of Marine Mammal Medicine*.

Geraci and Lounsbury, *Marine Mammals Ashore*.

National Oceanic and Atmospheric Administration, "Marine Mammal and Sea Turtle Stranding and Disentanglement Program."

Reynolds III, Perrin, Reeves, Montgomery, and Ragen, eds., *Marine Mammal Research*.

Twiss Jr. and Reeves, eds., *Conservation and Management of Marine Mammals*.

Questions to Consider

1. What are some of the personal reasons you might cite for rescuing a stranded marine mammal? How does your answer change if the animal is not an endangered species?

2. If you live in the United States, research in which NOAA region your home is located. If you live on the coast, where is the nearest marine mammal stranding response unit? To what animals do they commonly respond?

3. With a group of friends, discuss the ethics of investing time, effort, and money into rescuing a harp seal in the northeastern United States only to have it killed and eaten or harvested for its fur in maritime Canada.

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THE URBAN OCEAN: HUMAN IMPACT ON MARINE LIFE

With the human population ever increasing, our oceans are becoming more and more industrial, and our modern lives are having a substantial impact on marine mammal species—an impact that has led some to coin the term "urban whale." This lecture is about the current anthropogenic threats to marine mammals and what we are doing to mitigate those threats. The lecture will focus on the North Atlantic right whale, for whom the title "urban whale" was intended. In reality, however, many other species are threatened by human activity simply because our distributions overlap.

Using the Ocean as a Resource

- ◇ The 3 main ways that the ocean is used as a resource are as food, transportation, and energy.
- ◇ Fishing has had a varied history since the mid-19th century. Per species of fish, we have seen fisheries boom and bust. The list of species that are now overfished and commercially extinct is too long, indicating inadequate management methods, poor understanding of population dynamics, and unchecked greed.
- ◇ There are some bright lights on the horizon, especially in the case of comanagement, a system whereby fishermen work together with local authorities to self-manage their operations. Giving the fishermen some stewardship of the stocks seems to have mostly worked.
- ◇ Marine aquaculture, or mariculture, is another bright light. We can now successfully farm many species of invertebrate, such as mussels. In some cases, we can even grow fish, although we are still far from developing truly efficient fish culturing. Importantly, most of our fishing activity is limited to coastal shelves for biological, logistic, and political reasons.
- ◇ Turning from food to transportation, shipping around the world has increased over the past century and a half. With rising fuel costs, industries have turned to container fleets as a relatively inexpensive option for moving goods in bulk. And ships have become larger and faster. We now have fast ferries capable of speeds in excess of 100 kilometers per hour.
- ◇ New technologies also allow us to monitor global shipping. Large ships are required to carry a satellite-linked beacon known as the automatic identification system (AIS), which allows us to track these ships as they travel around the world.

- We can even generate graphics depicting ocean traffic based on AIS data. These graphics show us various choke points where ships jam together in tightly navigable spaces, such as the Suez or Panama Canal. And while there is plenty of traffic making transoceanic journeys, it's clear from AIS data that the majority of vessels stay close to the coastline, in shelf waters.

- In addition to its importance for transportation and food, the ocean continues to be a source of energy. Not only do we drill the seabed for fossil fuels, but it is now believed that various areas around North America may be ideal sites for wind farms. We are also developing technologies for wave and tidal energy.

- The distribution of such enterprises is within shelf water, principally for logistic reasons: It's much harder to anchor and drill in deep water, and getting energy generated from an offshore site to the mainland requires significant cabling.

The Urban Whale

- Although technically Arctic-adapted, mature North Atlantic right whales—so-called urban whales—head south and overwinter off the southern states of the U.S. Eastern Seaboard, where they give birth and suckle their young. Then, with the approach of spring and summer, they move northward to feeding grounds that include Cape Cod Bay and the Bay of Fundy.

- We know these movements relatively well because of ship and aerial surveys, as well as various listening technologies. A device developed in the late 1990s by Cornell University—known as the marine autonomous recording unit—is essentially an anchored underwater recording buoy that collects terabytes of acoustic data. When deployed as an array along a coastline, one can hear

vocalizing right whales as they move up and down the coast. In this way, we have been able to track their movements acoustically, but only after the fact because we have to wait to retrieve the buoy.

- A refinement of this is a permanently moored acoustic buoy that is connected to a cell phone antenna at the surface. Onboard recognition algorithms determine if right whales are being heard and then send that information back to the mainland.

- This sort of acoustic monitoring has not only been useful in confirming our understanding of where right whales are at various times of the year, but it has also revealed places where we did not expect them and therefore were not looking for them.

- The North Atlantic right whale is highly vulnerable to adverse interactions with humans because its behavior brings it into very close proximity with human activity.

The North Atlantic right whale population is highly endangered, numbering around 500 animals. In fact, the population of North Atlantic right whales is barely increasing—perhaps 100 or so animals in the past 15 years—because the number of mortalities that occur from year to year as a result of entanglements in fishing gear or whale-vessel strikes is in the same order of magnitude as the number of annual births.

There appears to be an unfortunate spatial and temporal coincidence of right whales and humans. In other words, as 2 species, we both use the same areas of the ocean—specifically, the inshore environment—at the same time.

Fisheries Management

- In the United States, the agency responsible for managing oceanic species is the National Oceanic and Atmospheric Administration (NOAA). Not only is NOAA bound by the Marine Mammal Protection Act to protect the North Atlantic right whale, but it is also responsible for issuing offshore fishing licenses.

- Conservation advocates in the late 1990s picked up on this seeming conflict of interest—that NOAA was licensing an activity that was impacting one of their own conservation mandates—and therefore threatened legal action. Perhaps as a result of this, the early 2000s saw a flurry of activity in NOAA-governed fishery management practices in an attempt to make fishing gear safe for whales.

- We invented weak links, points in the gear that would break if too much strain was put on them—for example, the strain generated by a struggling whale. We also modified how gear was set. In the 1990s, the Gulf of Maine lobster fishery was specifically identified as a potential concern for right whales. Fishermen often set multiple traps connected by a floating line—known as a groundline—that floated high enough in the water column that a whale might hit it.

- In the 2000s, the managers' reaction to this problem was to make that line neutrally or negatively buoyant so that it would remain on the seafloor. Fishermen were frustrated because this change meant that the line now chafed along the seafloor and could potentially break, resulting in the fisherman losing his gear.

- Managers also developed ways to close certain areas during seasons when right whales were known to be common, a technique known as seasonal area management. They also developed a management tool known as dynamic area management (DAM), whereby they could temporarily close an area to fishermen if high concentrations of whales were seen in the area.

- Overall, fishermen's reactions to these management strategies were mixed at best, and in some cases downright hostile. Regardless, all of these proposed strategies were eventually implemented. However, the sinking groundline rule did not improve entanglement rates in the way managers had hoped and was costly for the fishermen, and the DAM proved difficult to implement. Weak links and sinking groundline, however, have indeed become standards throughout the industry, despite complaints from fishermen.

- In response to the lack of impact of the groundline rule, managers started to look at vertical lines, which travel from the soaked gear to the surface. In 2014, NOAA implemented a rule that requires fishermen to set more lobster pots per string, which would reduce the number of vertical lines they could have in the water. Again, fishermen resisted this change, but it has been implemented. It's too soon to know if this has had an impact in reducing entanglement.

The relationship between fishermen, managers, conservation advocates, and scientists is not always a good one. Fishermen blame the scientists for not giving good data to the managers and blame the managers for being blinkered in their approach. Advocates believe the fishermen to be uncooperative, scientists complain that no one understands what science can and cannot do, managers feel extremely cornered and threatened by the advocates, and so on.

- Part of the solution is to create a sense of stewardship across the entire community. Scientists are now putting their best efforts into understanding how and why entanglement occurs, and fishermen are helping us design solutions that will have minimal impact on the fisheries.

Transportation Management

- Large-scale shipping is similarly problematic for North Atlantic right whales, again because the 2 overlap spatially and temporally. Here, perhaps we have seen more success. Ship strikes come either in the form of a collision, causing blunt force trauma, or through lacerations typically caused by a propeller.

- If an animal dies because of a ship strike, it is up to marine mammal stranding response teams to collect the data. Necropsy techniques continue to develop, and we now have ways to forensically examine wounds so that we can determine the kind and size of propeller that caused it and even take an educated guess on how fast the vessel was traveling when it hit the whale.

- Blunt force trauma causes bruising, internal bleeding, and broken bones, and some fascinating work has begun to extrapolate on the forces required to break whale bone, again helping us to think about the size and speed of the offending vessel.

- The slow speed of right whales, coupled with their apparent lack of awareness of the surrounding environment, seems to make them particularly vulnerable to ship strikes.

Recent evidence suggests that ships, in spite of their large size, may be actually quite difficult to hear. This is especially true when a whale is directly in front of a ship's path, where researchers have discovered an acoustic shadow zone. This so-called bow null effect means that if a whale is directly in front of a ship, it may have no idea that it's in danger.

- There are 2 strategies that we believe have been effective in reducing the probability of a ship's collision with a right whale. First, we have implemented speed zones. As ships approach areas of congestion where right whales are present, they can listen to broadcasts that provide the latest right whale sighting.

- There is a cell phone app called WhaleAlert that provides close to real-time right whale locations based on those cell-linked acoustic buoys mentioned previously. There is even a part of the app where local boaters can upload their own sightings and contribute to the warning system.

- Ships now have to reduce their speed to 10 knots or slower in certain areas regardless of current sightings. Slowing down is part of the solution to avoid hitting right whales—or at least giving them a chance to get out of the way before they're hit. The AIS system allows us to monitor whether ships are complying with the rules.

- In addition to speed zones, the second strategy is to move shipping lanes away from known concentrations of animals. Although it looks like an open ocean out there, vessels—especially large ones—must follow certain routes in and out of port. These routes are called traffic separation schemes (TSSs).

- A heroic effort by scientists in Canada managed to persuade the International Maritime Organization to move the TSS established in the Bay of Fundy, thereby reducing the chance of right whale collisions by 80%. This move was supported by the shipping industry, for whom it corresponded to a small diversion of 4 miles.

- Similar changes have been made to the TSS for Boston in the Gulf of Maine, and we now also have areas to be avoided (ATBAs), which are nonmandatory areas of known whale concentrations where we request the shipping industry refrain from entering unless absolutely necessary. Even though there is no legal consequence for entering an ATBA, they have been respected. Again, AIS has been used to monitor compliance.

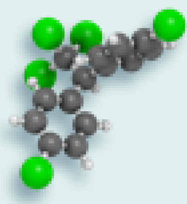
Pollution Management

- Human activities on land often have a price, and various chemicals end up in the ocean either through river runoff or through atmospheric transport that ends up precipitating over the ocean.

- Of principal concern here are the chemicals with a long half-life—that is, chemical compounds that take a long time to break down into their simpler harmless forms. Many industries now make use of various organic compounds called persistent organic pollutants that have very long half-lives.

◇ In some cases, we have known about the chemical's toxicity, and in others, it has been an unexpected negative consequence. Certain fertilizers are known to have long breakdown times, and flame-retardant chemicals are particularly toxic. The list of offenders seems endless but also includes various species of lead and mercury. Many chemicals often end up in a marine mammal's blubber. Sometimes they will remain inert, but if the animal metabolizes that blubber for any reason, the harmful chemicals go back into circulation.

In the 1940s and 1950s, we thought that dichlorodiphenyltrichloroethane (DDT) would be a useful chemical to fight mosquito infestations. It was not until the early 1970s that the substance was banned in the United States because of adverse side effects. By then, it was too late, and much of the DDT that had been used ended up washing into the local watersheds and out to sea.



◇ Apart from outright toxicity, we also know that some of these chemicals cause long-term immunosuppression; in other words, they impact an animal's ability to fight disease. Currently, most research is aimed at observing what these various pollutants do at a molecular level to gene expression.

◇ The solution to this problem has to be through regulation, but unfortunately the industries that produce these pollutants are often creating products that we as a society think that we need. For example, gasoline additives, which end up being vaporized and rained out on the ocean, help engines be more efficient.

◇ While we can regulate all we want in the United States, we have very little power to influence how other countries deal with pollution. The signing of the United Nations' Stockholm Convention on Persistent Organic Pollutants of 2001 was a huge step forward, although the U.S. Congress has yet to ratify the convention.

- Plastic has a very long half-life. Plastics can physically interfere with organisms, causing the death of marine mammals when they are ingested. In addition, microplastics can easily be accidentally ingested while organisms are feeding and can absorb other kinds of chemical pollution and act to concentrate it, exposing the organisms to other toxic effects.

- Sound pollution may be a strange concept, but not all pollutants have to be material in nature. We have been putting sound into the ocean since the birth of the Industrial Revolution. The level of general, unidentified sound in the ocean is referred to as ambient noise.

- There are plenty of natural contributors to ambient noise, such as various organisms—including marine mammals—as well as the sound of waves, rain, and earthquakes. However, especially at the level of low frequencies that travel great distances, we see the insidious influences of shipping, underwater construction, explosions, and other seismic surveying techniques.

- Many marine mammals depend on acoustics for communication and environmental orientation, particularly at low frequencies. So, the concern is that we are creating a noisy ocean that will either deafen the animals or drown out their communications.

- We know that chronic exposure to loud sounds over a long time can cause what audiologists call temporary threshold shift, a reference to the fact that an individual's hearing sensitivity curve shifts, meaning that certain sounds have to be much louder to be heard. Exposure to sharp, sudden loud sounds can cause permanent deafness, or permanent threshold shift.

- We now have clear evidence for both phenomena in marine mammals. If a sound is too loud, there can be serious implications for a marine mammal that depends on sound for essential life functions.

- The effect of sound preventing communication is known as masking, and this is probably the bigger concern when we think about the increase in ambient noise over the past 150 years. Marine mammals have evolved an acute sense of hearing. However, as background noises rise, it will become increasingly difficult to hear a signal.

- We believe that we now have evidence of animals vocalizing louder in an attempt to overcome this. Distances of propagation are almost certainly much lower than they used to be because of increases in ambient noise.

- It is extremely difficult to regulate ambient noise. Certainly, quieter boat engines will help. We now also regulate noisy industrial activities that occur close to marine mammal populations.

LECTURE SUPPLEMENTS

Readings

Carson, *Silent Spring*.

Dougherty and Hinerfeld, *Sonic Sea*.

Krauss and Rolland, eds., *The Urban Whale*.

Laist, *North Atlantic Right Whales*.

National Research Council, *Marine Mammal Populations and Ocean Noise*.

Parsons, *An Introduction to Marine Mammal Biology and Conservation*.

Reynolds III, Perrin, Reeves, Montgomery, and Ragen, eds., *Marine Mammal Research*.

Twiss Jr. and Reeves, eds., *Conservation and Management of Marine Mammals*.

Questions to Consider

1 Often, conservation issues arise as a product of conflicting human and animal needs. Using the example of the North Atlantic right whale, discuss with friends whether it is possible or even practical to prioritize one over the other. Repeat this exercise using the example of the vaquita.

2 Research the smartphone application WhaleAlert and its purpose.

3 Research the demise of the Chinese river dolphin, otherwise known as the baiji. What key human activities led to its extinction?

NOTE: Since this lecture was prepared, the number of right whales known to have died in 2017 has increased to 18 individuals, found in various states of decomposition off the coast of Atlantic Canada and the U.S. Eastern Seaboard. This unprecedented level of mortality invoked both governments to act quickly; in the United States, an Unusual Mortality Event was declared. Evidence implicated both the fishing and shipping industries as important contributors to this pulse of deaths.

Based on new models, the North Atlantic right whale population is now estimated at around 450 individuals, suggesting that while the population increased slightly in the first decade of this millennium, it is now in fact decreasing. Within this population, researchers estimate that only around 100 individuals are female, further limiting this species' ability to return from the brink of extinction. Efforts continue to reduce the impacts of shipping and fishing industries, although more animals now die from fishery interactions than from ship strike. Researchers continue to investigate ways to remove as much vertical fishing line from the water column as possible. In the meantime, the struggle of the "urban whale" has become even more acute.

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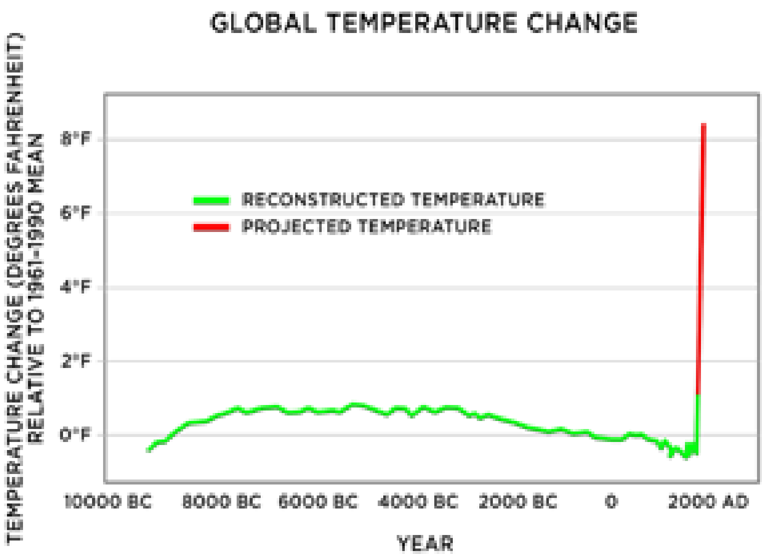
OUR ROLE IN THE OCEAN'S FUTURE

This lecture is about the power of human society to irrevocably change the course of this planet by affecting the environment and the biota within it. The term "Anthropocene extinction" is commonly applied to the extinction of terrestrial species because of the destruction of their habitat. But what does this mean in terms of the ocean? This lecture divides our concerns into 3 impacts: global climate change, ocean acidification, and overfishing.

Global Climate Change

- Global climate change is a contentious issue in the United States. Although we continue to debate the existence of climate change within our political system, from a scientific point of view, all the evidence points to the conclusion that climate change is accelerating and that we are the cause of that acceleration.

- Naysayers will claim that over geological time scales, the climate is always changing—and they're right. In the 1920s, Serbian astronomer Milutin Milankovitch proposed what we know as the Milankovitch cycles—that the Earth's orientation to the Sun varies naturally on scales ranging from 20,000 to 100,000 years, thus impacting the amount of insolation the Earth receives. We have since used this concept to explain the cyclic nature of ice ages.



- The planet does indeed go through natural periods of warming and cooling. Are we maybe just experiencing one of those natural upswings in temperature now? Unfortunately, the evidence suggests that this is not the case. An examination of global temperature anomalies over thousands of years does suggest such cycling, but around the middle of the 19th century, something goes horribly wrong with that line and it accelerates rapidly. That inflection around the 1850s and 1860s corresponds perfectly with an exponential increase in the use of fossil fuels from the birth of the Industrial Revolution.

- Burning fossil fuels releases 2 greenhouse gases—carbon dioxide and water vapor—that act to trap the planet's heat, causing atmospheric temperatures to rise. From a scientific perspective, then, climate change is accelerating due to humanity's influence through the production of greenhouse gases.

- What are some of the consequences for the ocean? If the atmosphere warms, then so will ocean water, but at a slower rate because water has a higher heat capacity than air.

- Researchers can monitor this ocean warming through satellite telemetry and direct measurements. These data are then input into models that incorporate knowledge of both oceanic and atmospheric circulation, as well as various assumptions about how we as a society might react to climate change, to see how the planet's climate might react.

- Once we have those models, we can then think about the potential impact to marine life. First, we need to consider the effect at the level of primary productivity. We now have data that suggest a good correlation between areas of the ocean that are warmer than we expect with decreased productivity. This is because surface warming creates a stratification of the water column, inhibiting the recycling of vital nutrients from the depths to the surface—nutrients that are essential for photosynthesis.

- ◇ Second, a majority of animal life in the ocean—invertebrates such as plankton as well as the vertebrate fish—are ectothermic. This means that they will reflect within their bodies the temperature of their surroundings. But those bodies have evolved over millions of years to create a physiology and metabolism that operates optimally in an ocean of "normal" temperature.

- ◇ Climate change is happening so rapidly that organisms don't have time to adapt through the process of natural selection. In reality, ocean temperatures have changed for eons, and animals have adapted through evolutionary time as appropriate. But the current change is happening way too quickly for organisms to adapt appropriately. We could be looking at extensive extinctions because of this.

- ◇ In the case of ectothermic nekton—that is, organisms capable of migration—we might see substantial shifts in distribution as species move to higher latitudes, where it is still colder. Even endotherms, such as whales and dolphins, in theory capable of tolerating some level of environmental change because they maintain their own internal body temperatures, might exceed their tolerance and be forced toward a more polar distribution.

- ◇ We might be already seeing these effects to some extent. The Gulf of Maine, on the East Coast of the United States, has recently been identified as one of the most rapidly warming patches of ocean anywhere in the world. Data now suggests that certain fisheries in the gulf—such as hake, flounder, and cod—may be impacted because of this change.

- ◇ There will also be more physical effects on the ocean as a whole. On a more global scale, we might expect sea levels to rise over time, for 2 reasons: First, the ice caps will begin to melt, coincidentally and irreversibly destroying polar habitat for a number of species. Second, sea levels will rise because of thermal expansion; warmer water occupies more space than colder water.

Using satellite telemetry, NASA has determined that since 1979, we have been losing sea ice at an annual average rate of 35,000 square kilometers, and this rate of loss is increasing, having doubled in the past 20 years. As a result of this and thermal expansion, sea level is now 6.5 centimeters higher on average than it was in the early 1990s.

- Sea level rise per se might not affect marine organisms drastically, although intertidal regions will shift inland, and sensitive ecosystems, such as mangroves and seagrass beds, may not have time to shift their distribution with rising sea levels. Corals that depend on their proximity to the sea surface to get oxygen through wave action may be drowned because they cannot grow as fast as sea level is rising.

- Finally, and perhaps most worrying, increasing ocean temperatures may totally shift the nature of oceanic thermohaline circulation, which moves vast masses of water around our ocean. As a consequence, heat is redistributed around our planet, a phenomenon known as the ocean conveyor. Researchers have suggested that the melting of the ice sheets covering Greenland may already have slowed the ocean conveyor.

- The impacts of an abrupt shutdown to the conveyor would be catastrophic but are very difficult to model. Temperatures in Europe and North America, for example, could plunge drastically. Sea life would be dramatically impacted, because oxygen could no longer be circulated around the ocean, and plankton stocks, at the heart of all marine food webs, might fail.

Ocean Acidification

- Unfortunately, there is a secondary effect of the accumulation of carbon dioxide in our atmosphere, one that might have more immediate and important consequences: ocean acidification, in which carbon dioxide combines with water to produce carbonic acid. We now know that the ocean has a certain capacity for holding carbon dioxide and resisting that increase in acidity—up to a point. The concern is that we have reached that point, and now we are starting to see pHs decrease in the oceans around us.

- This could be potentially disastrous. The metabolism of many organisms relies on the ocean having a relatively neutral pH, being neither acidic nor alkaline. If we move too far in the direction of acidity, organisms—especially phytoplankton and zooplankton—may simply not be able to function.

- Because of the profound impact acidification would have at the foundational trophic levels of the marine ecosystem, it would have a knock-on effect on all the organisms that depend on them. Any organism that makes a calcium carbonate shell as protection risks that structure being redissolved into the ocean if acidity gets too high. A combination of increases in ocean temperature and acidification is already starting to bleach corals worldwide, rendering them lifeless.

A recent study suggests that coral populations along the Great Barrier Reef have declined by 5% in the past 30 years because of bleaching events and that such events are likely to continue under any but the least severe of the warming scenarios.

Overfishing

- Before the Industrial Revolution, overfishing was rare, but it wasn't impossible. There is plenty of historical evidence to suggest that many fish stocks were very sensitive to preindustrial fishing pressure, especially in years when environmental conditions were less favorable to population growth and replacement.

- But the Industrial Revolution was a game changer. Boats became stronger and more powerful and could range farther for longer periods of time. Instead of relying on humans to haul a line, one could use a hydraulic winch instead. Nets became larger and targeted larger catches. Onboard refrigeration allowed ships to take more fish. With the birth of electronics, we developed tools that could help us find the fish.

- Each of these developments was another nail in the coffin for the sustainability of fish species. Lack of monitoring and enforcement encouraged bycatch and discard because there were no consequences to such practices.

- These factors, coupled with an almost-arrogant assumption that we could mathematically predict fishing levels that would be sustainable, were a recipe for disaster. Today, a majority of the world's fisheries are either overexploited or have collapsed.

- Ocean community structure looks very different now than it did 150 years ago, due to what is called the trophic cascade effect. This arises because we as a society tend to favor the larger, higher-trophic-level species, such as tuna or swordfish. So, we target them first. When they are all gone, we go for the next-best thing, and when *they're* gone, then we go for the next best after that, and so on. The marine community that is left is therefore, on average, represented by smaller and smaller, less desirable fish.

In New England, lobster was once considered trash fish, a species that is not considered worthy of harvest. In Victorian times, well-to-do homes would not even dream of feeding their servants lobster—it would be an insult to them.

But many fisheries in New England are now so overexploited that we have no choice but to fish lower down the food chain. Therefore, lobster is now favored as a delicacy and is an economic mainstay for the tourist industry in New England.

Making Progress

- The ocean is not an infinite resource. It is finite, and humans have the power to create serious impact. But there is light at the end of this tunnel. Over the past 20 years, we have become more and more aware of our role in climate change. And while this continues to be a political issue in the United States, the rest of the world is developing a much more progressive philosophy.

- On a yearly basis, the world's nations meet to discuss and sign treaties that commit them to actions that will combat the causes of climate change. The United States frequently declines to sign such treaties; in 2017, it withdrew from the 2016 Accord de Paris.

- But pretty much all of the remaining nations have signed the Paris accord, which calls for countries to reduce fossil fuel emissions to "level[s] that would prevent dangerous anthropogenic interference with the climate system." The fact that most of the world has committed to pursuing such a goal is amazing progress.

- As for overfishing, we are trying to meet the problem with both local and global solutions. Globally, we have created broad treaties that help coordinate management of species that cross international boundaries.

- More locally, we are beginning to realize that there are more effective ways to manage fisheries. Rather than focusing on single-species management, we attempt instead to manage ecosystems—that is, we consider the effects of removing portions of one species on all other species in that ecosystem. This is a much more realistic management strategy.

- ◇ Many fisheries now also adopt the so-called precautionary principle—that is, if we do not understand the impacts of a particular management method, then that method isn't adopted. The phrase "long-term sustainability" is now commonplace among managers.

- ◇ Historically, there has been intense distrust between fishermen, scientists, and the government. And this has sometimes hindered our ability to manage fisheries effectively. One solution that might help reduce this problem is comanagement. In this system, fishermen are invited to bring their expertise and experience to the management table, and fishermen and the government work together to manage the fishery.

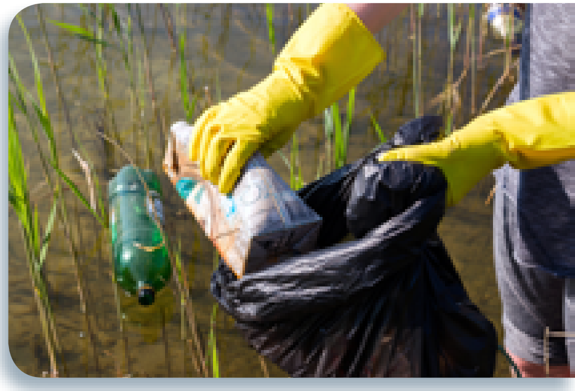
What Can You Do?

- ◇ It is not the fisherman's ocean, nor is it the government's ocean—it's *our* ocean. We, the people, can tell those that represent us that we want and need a sustainable ocean. Vote for representatives that best represent how you think our oceans should be managed. If they don't understand a problem, then demand their understanding. They work for you; you pay their salary. If they don't listen to you, then don't vote for them.

- ◇ When you buy fish at the supermarket, vote with your wallet and buy only sustainably fished species—species that you have researched. If the store can't tell you if a fish has been caught in a certified sustainable fishery, then don't buy it. Better still, walk out of the store and let them know that you'll be back when they start taking responsibility for what they sell. Do the same at restaurants. Consider supporting local fishermen by buying locally and perhaps from a cooperative—you'll get a much higher-quality fish that way, too.

- Think about your environmental footprint. Recycle, always. On your next trip to the shops, do you need to take the car, or could you use a bicycle? If you're thinking about building a house, consider installing solar power and sell the excess power generated back to the grid.

- In general, take steps in your life to minimize your impact on the environment and on the ocean that nurtures us. By doing so, you will play an important part in maintaining the marvelous diversity of life in the ocean.



LECTURE SUPPLEMENTS

Readings

Earle, *The World Is Blue*.

Food and Agriculture Organization of the United Nations, "The 2016 State of the World's Fisheries and Aquaculture."

World Wildlife Fund, "Living Planet Report 2016."

Worm, Lotze, Jonsen, and Muir, "The Future of Marine Animal Populations."

Web Resources

Intergovernmental Panel on Climate Change, https://www.ipcc.ch.

Monterey Bay Aquarium Seafood Watch, http://www.seafoodwatch.org/.

Ocean Health Index, http://www.oceanhealthindex.org/.

Smithsonian Institution, "Ocean Portal: Acidification," http://ocean.si.edu/conservation/acidification.

————, "Ocean Portal: Climate Change," http://ocean.si.edu/conservation/climate-change.

Questions to Consider

1. Research the Intergovernmental Panel on Climate Change (www.ipcc.ch). What is the purpose of this institution?
2. Research the principles of the 2016 Paris accord. Why was it so revolutionary in comparison to previous international meetings on climate?
3. Research the role of the Food and Agriculture Organization of the United Nations (http://www.fao.org) in monitoring the world's fisheries. What are the general findings of the executive summary of their latest report?
4. Research the Living Planet Index (http://www.livingplanetindex.org/). What are its general conclusions, according to its most recent report?
5. Research the Ocean Health Index (http://www.oceanhealthindex.org/). What are its general findings?
6. Research what you can do in terms of consumerism to promote a sustainable planet.

BIBLIOGRAPHY

Acheson, James M. *Capturing the Commons: Devising Institutions to Manage the Maine Lobster Industry*. Lebanon, NH: University Press of New England, 2003.

Amaral-Zettler, Linda, Luis Felipe Artigas, John Baross, Loka Bharathi P. A., Antje Boetius, Dorairajasingam Chandramohan, Gerhard Herndl, Kazuhiro Kogure, Phillip Neal, Carlos Pedrós-Alió, Alban Ramette, Stefan Schouten, Lucas Stal, Anne Thessen, Jan de Leeuw, and Mitchell Sogin. "A Global Census of Marine Microbes." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 223–245. Oxford, UK: Wiley-Blackwell, 2010.

Au, Whitlow W. L. *The Sonar of Dolphins*. New York: Springer Verlag, 1993.

Au, Whitlow W. L., and Mardi C. Hastings. *Principles of Marine Bioacoustics*. New York: Springer Science, 2008.

Au, Whitlow W. L., N. Arthur Popper, and Richard R. Fay, eds. *Hearing by Whales and Dolphins*. New York: Springer Verlag, 2000.

Baker, Maria C., Eva Z. Ramirez-Llodra, Paul A. Tyler, Christopher R. German, Antje Boetius, Erik E. Cordes, Nicole Dubilier, Charles R. Fisher, Lisa A. Levin, Anna Metaxas, Ashley A. Rowden, Ricardo S. Santos, Tim M. Shank, Cindy L. Van Dover, Craig M. Young, and Anders Warén. "Biogeography, Ecology, and Vulnerability of Chemosynthetic Ecosystems in the Deep Sea." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 161–182. Oxford, UK: Wiley-Blackwell, 2010.

Berta, Annalisa, James L. Sumich, and Kit M. Kovacs. *Marine Mammals: Evolutionary Biology*. 3rd ed. London: Academic Press, 2015.

Block, Barbara A., Daniel P. Costa, and Steven J. Bograd. "A View of the Ocean from Pacific Predators." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 291–311. Oxford, UK: Wiley-Blackwell, 2010.

Bone, Quentin, and Richard H. Moore. *Biology of Fishes*. 3rd ed. New York: Taylor and Francis, 2008.

Boyd, Ian L., W. Don Bowen, and Sara J. Iverson, eds. *Marine Mammal Ecology and Conservation: A Handbook of Techniques*. New York: Oxford University Press, 2010.

Brakes, Philippa, and Mark P. Simmonds, eds. *Whales and Dolphins: Cognition, Culture, Conservation and Human Perceptions*. London: Earthscan, 2011.

Bucklin, Ann, Shuhei Nishida, Sigrid Schnack-Schiel, Peter H. Wiebe, Dhugal Lindsay, Ryugi J. Machida, and Nancy J. Copley. "A Census of Zooplankton of the Global Ocean." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 247–265. Oxford, UK: Wiley-Blackwell, 2010.

Burns, John J., J. Jerome Montague, and Cleveland J. Cowles, eds. *The Bowhead Whale*. Lawrence, KS: Allen Press, 1993.

Carson, Rachel. *Silent Spring*. 1962. Reprint, Boston, MA: Houghton-Mifflin Company, 2002.

Castellani, Claudia, and Martin Edwards, eds. *Marine Plankton: A Practical Guide to Ecology, Methodology, and Taxonomy*. Oxford: Oxford University Press, 2017.

Castellini, Michael A., and Jo-Ann Mellish, eds. *Marine Mammal Physiology: Requisites for Ocean Living*. Boca Raton, FL: CRC Press, 2015.

Castro, Peter, and Michael E. Huber. *Marine Biology*. 9th ed. New York: McGraw Hill, 2012.

Cole, Brandon, and Scott W. Michael. *Reef Life: A Guide to Tropical Marine Life*. Richmond Hill, ON: Firefly Books, 2013.

Coleridge, Samuel Taylor. *The Rime of the Ancient Mariner*. Mineola, NY: Dover Publications, 1970.

Coslow, Tony. *The Silent Deep: The Discovery, Ecology and Conservation of the Deep Sea*. Chicago: University of Chicago Press, 2007.

Cowperthwaite, Gabriela. *Blackfish*. DVD. Magnolia Home Entertainment, 2013.

Cramer, Deborah. *Smithsonian Ocean: Our Water, Our World*. Washington, DC: Smithsonian Institution Scholarly Press, 2008.

Dierauf, Leslie A., and Francis M. D. Gulland, eds. *CRC Handbook of Marine Mammal Medicine*. Boca Raton, FL: CRC Press, 2001.

Dizon, Andrew E., Susan J. Chivers, and William F. Perrin, eds. *Molecular Genetics of Marine Mammals*. Lawrence, KS: Allen Press, 1997.

Dolin, Eric. *Leviathan: The History of Whaling in America*. New York: W. W. Norton and Company, 2008.

Dougherty, Michelle, and Daniel Hinerfeld. *Sonic Sea*. DVD. Discovery Impact, 2016.

Earle, Sylvia. *The World Is Blue: How Our Fate and the Ocean's Are One*. Washington, DC: National Geographic Books, 2010.

Ebbe, Brigitte, David S. M. Billett, Angelika Brandt, Kari Ellingsen, Adrian Glover, Stefanie Keller, Marina Malyutina, Pedro Martinez Arbizu, Tina Molodtsova, Michael Rex, Craig Smith, and Anastasios Tselepides. "Diversity of Abyssal Marine Life." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 139–160. Oxford, UK: Wiley-Blackwell, 2010.

Ellis, Richard. *Men and Whales*. London: Robert Hale Ltd, 1991.

Enticott, Jon. *Seabirds of the World: The Complete Reference*. Mechanicsburg, PA: Stackpole Books, 1997.

Estes, James, Douglas DeMaster, Daniel Doak, Terrie Williams, and Robert Brownell. *Whales, Whaling, and Ocean Ecosystems*. Berkeley: University of California Press, 2007.

Etchegary, Gus. *Empty Nets: How Greed and Politics Wiped Out the World's Greatest Fishery*. St. John's, NL: Boulder Publications, 2013.

Evans, Peter G. H., and Juan A. Raga, eds. *Marine Mammals: Biology and Conservation*. New York: Kluwer Academic/Plenum Publishers, 2001.

Fogg, G. E. *The Biology of Polar Habitats*. Oxford: Oxford University Press, 1998.

Folkens, Pieter, Randall R. Reeves, Brent S. Stewart, Phillip J. Clapham, and James A. Powell. *Guide to Marine Mammals of the World*. New York: Alfred A. Knopf Inc., 2002.

Ford, John, Graeme Ellis, and Kenneth Balcomb. *Killer Whales: The Natural History and Genealogy of* Orcinus Orca *in British Columbia and Washington State*. Vancouver: University of British Columbia Press, 1999.

Fuller, Errol. *The Great Auk*. New York: Harry N. Abrams Publishing, 1999.

Gelb, David. *Jiro Dreams of Sushi*. DVD. Magnolia Home Entertainment, 2012.

Geraci, Joseph R., and Valerie J. Lounsbury. *Marine Mammals Ashore: A Field Guide for Strandings*. 2nd ed. Sparks, MD: E. John Schmitz and Sons Inc., 2005.

Gradinger, Rolf, Bodil A. Bluhm, Russell R. Hopcroft, Andrey V. Bebruk, Ksenia Kosobokova, Boris Sirenko, and Jan M. Węslaswski. "Marine Life in the Arctic." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 183–202. Oxford, UK: Wiley-Blackwell, 2010.

Gutt, Julian, Graham Hosie, and Michael Stoddart. "Marine Life in the Antarctic." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 203–220. Oxford, UK: Wiley-Blackwell, 2010.

Hansom, James D., and John E. Gordon. *Antarctic Environments and Resources: A Geographical Perspective*. Harlow, UK: Pearson Education, 1998.

Hargrove, John, and Howard Chua-Eoan. *Beneath the Surface: Killer Whales, SeaWorld, and the Truth beyond Blackfish*. New York: St. Martin's Griffin Publishers, 2016.

Heyning, John E. *Whales, Dolphins and Porpoises*. Seattle: University of Washington Press, 1995.

Higham, James, Lars Bejder, and Rob Williams, eds. *Whale-Watching: Sustainable Tourism and Ecological Management*. Cambridge, UK: Cambridge University Press, 2014.

Hoezel, A. Rus, ed. *Marine Mammal Biology: An Evolutionary Approach*. Oxford, UK: Blackwell Publishing, 2002.

Hoyt, Erich. *Marine Protected Areas for Whales, Dolphins and Porpoises*. New York: Earthscan, 2011.

Jackson, Jeremy, Karen Alexander, and Enric Sala, eds. *Shifting Baselines: The Past and the Future of Ocean Fisheries*. Washington, DC: Island Press, 2011.

Jakobsson, Daniel, ed. *Fisheries, Aquaculture and Marine Mammals: Interrelationship, Background and Issues*. New York: Nova Science Publishers Inc., 2010.

Jefferson, Thomas A., Marc A. Webber, and Robert L. Pitman. *Marine Mammals of the World: A Comprehensive Guide to Their Identification*. 2nd ed. London: Academic Press, 2015.

Jefferson, Thomas A., Stephen Leatherwood, and Marc A. Weber. *Marine Mammals of the World*. Rome, IT: United Nations Food and Agricultural Organization, 1993.

Jennings, Simon, Michael J. Kaiser, and John D. Reynolds. *Marine Fisheries Ecology*. Oxford, UK: Blackwell Publishing, 2001.

Johnson, Tora. *Entanglements: The Intertwined Fates of Whales and Fishermen*. Gainesville, FL: University Press of Florida, 2005.

Johnson, William S., and Dennis M. Allen. *Zooplankton of the Atlantic and Gulf Coasts: A Guide to Their Identification and Ecology*. Baltimore, MD: Johns Hopkins University Press, 2005.

Junger, Sebastian. *The Perfect Storm: A True Story of Men against the Sea*. New York: W. W. Norton and Co., 2009.

Kaiser, Michael J., Martin J. Attrill, Simon Jennings, David N. Thomas, David K. A. Barnes, Andrew S. Brierly, Jan G. Hiddink, Hermanni Kaartokallio, Nicholas V. C. Polunin, and David G. Raffaelli. *Marine Ecology: Processes, Systems and Impacts*. Oxford: Oxford University Press, 2011.

Kalland, Arne. *Unveiling the Whale: Discourses on Whales and Whaling.* New York: Berghan Books, 2012.

Kastelein, Ronald A., Jeanette A. Thomas, and Paul E. Natchigall, eds. *Sensory Systems of Aquatic Mammals*. Worden, NL: De Spil Publishers, 1994.

King, Michael. *Fisheries Biology, Assessment and Management*. 2nd ed. Oxford, UK: Blackwell Publishing, 2007.

Klepac, Ariana, ed. *The Whale's Companion: The Whale in Legend, Art and Literature*. Millers Point, NSW: Pier 9 Publishers, 2008.

Klimley, A. Peter. *The Biology of Sharks and Rays*. Chicago: University of Chicago Press, 2013.

Knowlton, Nancy. *Citizens of the Sea: Wondrous Creatures from the Census of Marine Life*. Washington, DC: National Geographic Books, 2010.

Knowlton, Nancy, Russell E. Brainard, Rebecca Fisher, Megan Moews, Laetitia Plaisance, and M. Julian Caley. "Coral Reef Biodiversity." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 65–77. Oxford, UK: Wiley-Blackwell, 2010.

Krauss, Scott D., and Rosalind M. Rolland, eds. *The Urban Whale: North Atlantic Right Whales at the Crossroads*. Cambridge, MA: Harvard University Press, 2007.

Kurlansky, Mark. *Cod: A Biography of the Fish That Changed the World*. London: Penguin Books, 1998.

Laist, David. *North Atlantic Right Whales: From Hunted Leviathan to Conservation Icon*. Baltimore, MD: Johns Hopkins University Press, 2017.

Liem, Karel, William Bemis, Warren Walker, and Lance Grande. *Functional Anatomy of the Vertebrates: An Evolutionary Perspective*. 3rd ed. Pacific Grove, CA: Brooks Cole, 2000.

Lien, J., and S. K. Katona. *A Guide to the Photographic Identification of Individual Whales*. St. John's, NL: Breakwater Press, 1990.

Liss, Steve, Andy Laub, and David Abel. *Sacred Cod: The Fight for a New England Tradition*. DVD. Discovery Impact Films, 2017.

Mann, Janet, Richard C. Connor, Peter L. Tyack, and Hal Whitehead, eds. *Cetacean Societies: Field Studies of Dolphins and Whales*. Chicago: University of Chicago Press, 2000.

Mann, Ken H. *Ecology of Coastal Waters: With Implications for Management*. Malden, MA: Blackwell Science, 2000.

Margulis, Lynn, and Dorion Sagan. *What Is Life?* Berkeley: University of California Press, 2000.

Margulis, Lynn, and M. Dolan. *Early Life: Evolution on the Precambrian Earth*. 2nd ed. Sudbury, MA: Jones and Bartlett Publishing, 2002.

Martin, Stephen. *The Whale's Journey*. Crows Nest, AU: Allen and Unwin Publishing, 2001.

Martinez, Andrew J. *Marine Life of the North Atlantic: Canada to New England*. 2nd ed. Camden, ME: Downeast Books, 1999.

Matthiessen, Peter, and Birgit Bateman. *End of the Earth: Voyages to Antarctica*. Washington, DC: National Geographic Books, 2004.

McCalman, Iain. *The Reef: A Passionate History—The Great Barrier Reef from Captain Cook to Climate Change*. New York: Scientific American/ Farrar, Strauss and Giroux, 2015.

McIntyre, Alasdair D., ed. *Life in the World's Oceans: Diversity, Distribution and Abundance*. Oxford, UK: Wiley-Blackwell, 2010.

Melville, Herman. *Moby Dick*. Reprint ed. Ware, UK: Wordsworth Editions Ltd., 1999.

Miller, Charles B., and Patricia A. Wheeler. *Biological Oceanography*. 2nd ed. Chichester, UK: Wiley-Blackwell, 2012.

Mladenov, Philip. *Marine Biology: A Very Short Introduction*. Oxford: Oxford University Press, 2013.

Mora, Camilo, Derek P. Tittensor, Sina Adl, Alastair G. B. Simpson, and Worm Boris. "How Many Species Are There on Earth and in the Ocean?" *PLoS Biology* 9, no. 8 (2011): e1001127.

Moyle, Peter B., and Joseph J. Cech Jr. *Fishes: An Introduction to Ichthyology*. 5th ed. Upper Saddle River, NJ: Prentice Hall, 2004.

Mulvaney, Kieran. *Ice Bear: A Natural and Unnatural History of the Polar Bear*. London: Hutchinson Press, 2011.

Murray, Rupert. *End of the Line*. DVD. Docurama, 2010.

National Research Council. *Marine Mammal Populations and Ocean Noise: Determining When Noise Causes Biologically Significant Effects*. Washington, DC: National Academy of Sciences, 2005.

————. *Marine Mammals and Low Frequency Sound*. Vol. 146. Washington, DC: National Academy Press, 2000.

National Resources Defense Council. *Sounding the Depths: Supertankers, SONAR and the Rise of Undersea Noise*. New York: National Resources Defense Council, 1999.

Nouvian, Claire. *The Deep: The Extraordinary Creatures of the Abyss*. Chicago: University of Chicago Press, 2007.

O'Reilly, Jessica. *The Technocratic Antarctic: An Ethnography of Scientific Expertise and Environmental Governance*. Ithaca, NY: Cornell University Press, 2017.

Parsons, Edward C. M. *An Introduction to Marine Mammal Biology and Conservation*. Burlington, MA: Jones and Bartlett Learning, 2013.

Pauly, Daniel, and Jay MacLean. *In a Perfect Ocean: The State of Fisheries and Ecosystems in the North Atlantic Ocean*. Washington, DC: Island Press, 2003.

Philander, S. George. *Our Affair with El Niño*. Princeton, NJ: Princeton University Press, 2004.

Philbrick, Nathaniel. *In the Heart of the Sea*. London: Penguin Books, 2001.

Ponganis, Paul J. *Diving Physiology of Marine Mammals and Seabirds*. Cambridge, UK: Cambridge University Press, 2015.

Psihoyos, Louie. *The Cove*. DVD. Lions Gate Studios, 2009.

Read, Andrew J., Piet R. Wiepkema, and Paul E. Natchigall, eds. *The Biology of the Harbor Porpoise*. Worden, NL: De Spil Publishers, 1997.

Reynolds, John. E., III, and Sentiel A. Rommel, eds. *Biology of Marine Mammals*. Washington, DC: Smithsonian Institution Scholarly Press, 1999.

Reynolds, John. E., III, William F. Perrin, Randall R. Reeves, Suzanne Montgomery, and Timothy J. Ragen, eds. *Marine Mammal Research: Conservation beyond Crisis*. Baltimore, MD: Johns Hopkins University Press, 2005.

Richardson, W. John, Charles R. Greene Jr., Charles I. Malme, and Denis H. Thomson. *Marine Mammals and Noise*. San Diego, CA: Academic Press, 1995.

Riedman, Marianne. *The Pinnipeds: Seals, Sea Lions and Walruses*. Berkeley: University of California Press, 1990.

Rose, George A. *Cod: The Ecological History of the North Atlantic Fisheries*. St. John's, NL: Breakwater Books Ltd., 2007.

Rosenfeld, Anne. *The Intertidal Wilderness: A Photographic Journey through Pacific Coast Tidepools*. Berkeley: University of California Press, 2002.

Safina, Carl. *Eye of the Albatross: Visions of Hope and Survival*. New York: Holt Paperbacks, 2003.

———. *Voyage of the Turtle: In Pursuit of the Earth's Last Dinosaur.* New York: Holt Paperbacks, 2007.

Sardet, Christian. *Plankton: Wonders of the Drifting World*. Chicago: University of Chicago Press, 2015.

Schreiber, E. A., and J. Burger. *Biology of Marine Birds*. Boca Raton, FL: CRC Press, 2001.

Shirihai, Hadoram. *A Complete Guide to Antarctic Wildlife: Birds and Marine Mammals of the Antarctic Continent and Southern Ocean*. Degerby, FI: Alula Press, 2002.

Skomal, Greg. *The Shark Handbook: The Essential Guide for Understanding the Sharks of the World*. 2nd ed. Kennebunkport, ME: Cider Mill Press, 2016.

Spotila, James R. *Sea Turtles: A Complete Guide to Their Biology, Behavior and Conservation*. Baltimore, MD: Johns Hopkins University Press, 2004.

Stirling, Ian. *Polar Bears: The Natural History of a Threatened Species*. Markham, ON: Fitzhenry and Whiteside, 2011.

Stow, Dorrik. *Oceans: An Illustrated Reference*. Chicago: University of Chicago Press, 2006.

Supin, Alexander Y., Vladimir V. Popov, and Alla M. Mass, eds. *The Sensory Physiology of Aquatic Mammals*. Dordrecht, NL: Kluwer Academic Publishers, 2001.

Thewissen, J. G. M. Hans. *The Walking Whales*. Oakland: University of California Press, 2014.

Thewissen, J. G. M. Hans, ed. *The Emergence of Whales: Evolutionary Patterns in the Origin of Cetacea*. New York: Plenum Press, 1998.

Thomas, Jeanette, A., and Ronald A. Kastelein, eds. *Sensory Abilities of Cetaceans: Laboratory and Field Evidence*. New York: Plenum Press, 1990.

Thomas, Jeanette, A., F. Cynthia Moss, and Marianne Vater, eds. *Echolocation in Bats and Dolphins*. Chicago: University of Chicago Press, 2004.

Thomas, Jeanette, A., Ronald A. Kastelein, and Alexander Y. Supin, eds. *Marine Mammal Sensory Systems*. New York: Plenum Press, 1991.

Townsend, David W. *Oceanography and Marine Biology: An Introduction to Marine Science*. Sunderland, MA: Sinauer Publishers, 2012.

Twiss, John R., Jr., and Randall R. Reeves, eds. *Conservation and Management of Marine Mammals*. Washington, DC: Smithsonian Institution Scholarly Press, 1999.

Vallis, Geoffrey. *Climate and Oceans*. Princeton Primers in Climate. Princeton, NJ: Princeton University Press, 2010.

Van Dover, Cindy L. *The Ecology of Deep Sea Hydrothermal Vents*. Princeton, NJ: Princeton University Press, 2000.

Whitehead, Hal. *Sperm Whales: Social Evolution in the Ocean*. Chicago: University of Chicago Press, 2003.

Whitehead, Hal, and Luke Rendell. *The Cultural Lives of Whales and Dolphins*. Chicago: University of Chicago Press, 2015.

Worm, Boris, Heike K. Lotze, Ian Jonsen, and Catherine Muir. "The Future of Marine Animal Populations." In *Life in the World's Oceans: Diversity, Distribution and Abundance*, edited by Alasdair D. McIntyre, 315–353. Oxford, UK: Wiley-Blackwell, 2010.

Worsley, Frank A. *Endurance*. New York: W. W. Norton and Co., 1931.

Zimmer, Carl. *At the Water's Edge: Fish with Fingers, Whales with Legs*. New York: Simon and Schuster, 1998.

WEB RESOURCES

Center for Coastal Studies. "Marine Animal Entanglement Response."
http://coastalstudies.org/whale-rescue/.

Commission for the Conservation of Antarctic Marine Living Resources.
https://www.ccamlr.org/.

Convention for Migratory Species. "Memorandum of Understanding on the Conservation of Migratory Sharks."
http://www.cms.int/sharks/en.

Florida Museum. "International Shark Attack Files."
www.floridamuseum.ufl.edu/fish/isaf/home/.

Food and Agriculture Organization of the United Nations. "The 2016 State of the World's Fisheries and Aquaculture: Contributing to Food Security and Nutrition for All." Food and Agriculture Organization of the United Nations, Rome, 2016.
http://www.fao.org/3/a-i5555e.pdf.

Intergovernmental Panel on Climate Change.
https://www.ipcc.ch.

Maine Department of Marine Resources. "Maine Lobster."
http://www.maine.gov/dmr/science-research/species/lobster/.

Marine Stewardship Council: Certified Sustainable Seafood.
https://www.msc.org.

Monterey Bay Aquarium Seafood Watch.
http://www.seafoodwatch.org/.

Muth, Felicity. “Crows Take a Look in the Mirror.” *Scientific American*, 2011.
https://blogs.scientificamerican.com/not-bad-science/crows-take-a-look-in-the-mirror/.

National Geographic Society. “Krill.”
http://www.nationalgeographic.com/animals/invertebrates/group/krill/.

National Oceanic and Atmospheric Administration. “Harmful Algal Blooms: Tiny Organisms with a Toxic Punch.”
https://oceanservice.noaa.gov/hazards/hab/.

———. “Marine Mammal and Sea Turtle Stranding and Disentanglement Program.”
https://www.greateratlantic.fisheries.noaa.gov/protected/stranding/.

———. “The Marine Mammal Protection Act.”
http://www.nmfs.noaa.gov/pr/laws/mmpa/.

Ocean Health Index.
http://www.oceanhealthindex.org/.

Secretariat of the Antarctic Treaty. “The Antarctic Treaty.”
http://www.ats.aq/e/ats.htm.

Smithsonian Institution. “Ocean Portal: Acidification.”
http://ocean.si.edu/conservation/acidification.

———. “Ocean Portal: Beaches.”
http://ocean.si.edu/ocean-life-ecosystems/beaches.

———. “Ocean Portal: Birds.”
http://ocean.si.edu/ocean-life-ecosystems/birds.

———. “Ocean Portal: Climate Change.” http://ocean.si.edu/conservation/climate-change.

———. “Ocean Portal: Coral Reefs.” http://ocean.si.edu/ocean-life-ecosystems/coral-reefs-0.

———. “Ocean Portal: Fish.” http://ocean.si.edu/ocean-life-ecosystems/fish.

———. “Ocean Portal: Invertebrates.” http://ocean.si.edu/ocean-life-ecosystems/invertebrates.

———. “Ocean Portal: Mammals.” http://ocean.si.edu/ocean-life-ecosystems/mammals.

———. “Ocean Portal: Mangroves.” http://ocean.si.edu/ocean-life-ecosystems/mangrove-forests.

———. “Ocean Portal: Overfishing.” http://ocean.si.edu/conservation/overfishing.

———. “Ocean Portal: Planet Ocean.” http://ocean.si.edu/planet-ocean.

———. “Ocean Portal: Plankton.” http://ocean.si.edu/ocean-life-ecosystems/plankton.

———. “Ocean Portal: Plants and Algae.” http://ocean.si.edu/ocean-life-ecosystems/plants-algae.

———. “Ocean Portal: Poles.” http://ocean.si.edu/ocean-life-ecosystems/poles.

———. “Ocean Portal: Reptiles.” http://ocean.si.edu/ocean-life-ecosystems/reptiles.

———. “Ocean Portal: Sharks and Rays.”
http://ocean.si.edu/ocean-life-ecosystems/sharks-rays.

———. “Shark Finning: Sharks Turned Prey.”
http://ocean.si.edu/ocean-news/shark-finning-sharks-turned-prey.

———. “The Division of Fishes.”
http://vertebrates.si.edu/fishes/.

The Society for Marine Mammalogy.
https://www.marinemammalscience.org/.

Thompson, Andrea. “Krill Are Disappearing from Antarctic Waters.” *Scientific American*, 2016.
https://www.scientificamerican.com/article/krill-are-disappearing-from-antarctic-waters/.

United States Environmental Protection Agency. “Harmful Algal Blooms.”
https://www.epa.gov/nutrientpollution/harmful-algal-blooms.

World Wildlife Fund. “Living Planet Report 2016: Risk and Resilience in a New Era.” WWF International, Gland, Switzerland, 2016.
http://www.wwf.org.uk/sites/default/files/2016-10/LPR_2016_fullreport_spread_low_res.pdf.

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